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The Carpolestidae

Early Tertiary Primates from North America

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THE CARPOLESTIDAE
EARLY TERTIARY PRIMATES FROM NORTH AMERICA

KENNETH D. ROSE[1]

Dedicated to
the memory of
Professor Glenn Lowell Jepsen
1903–1974

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ABSTRACT. The Carpolestidae were archaic primates of the superfamily Plesiadapoidea. They have been recovered from strata of Middle Paleocene (Torrejonian) to early Eocene (Wasatchian) age in western North America. Although known only from jaws, teeth, and a few cranial fragments, carpolestids have very characteristic dentitions by which they are easily recognized. Most diagnostic are the enlarged, serrate P_4, and the enlarged, polycuspate P^3 and P^4.

The systematic revision includes emended diagnoses for all taxa. Three genera, *Elphidotarsius, Carpodaptes,* and *Carpolestes,* are recognized. There are nine valid species: two in *Elphidotarsius,* five in *Carpodaptes* (including one new species), and two in *Carpolestes. Saxonella,* a Middle Paleocene primate from Europe originally described as a carpolestid, is an aberrant plesiadapoid, here placed in a family separate from carpolestids and plesiadapids.

New material described provides the first published information on the upper teeth of *Elphidotarsius,* the lower incisors of *Elphidotarsius* and *Carpolestes,* the anterior teeth of *Carpolestes,* the posterior part of the mandible of *Carpodaptes,* and the snout of *Carpolestes,* as well as additional evidence bearing on dental formulae and intraspecific variability.

Analysis of wear facets indicates that the molars of carpolestids resemble those of plesiadapids not only morphologically, but also functionally; they were used in the shearing (Phase I) and grinding (Phase II) stages of mastication. The specialized premolars were probably most important during the "puncture-crushing" stage, when the bladelike P_4 was used to tear or cut food. They were less important during Phase I and probably ineffective during Phase II.

The three genera, *Elphidotarsius, Carpodaptes,* and *Carpolestes,* form a natural sequence both morphologically and stratigraphically, indicating that they are representatives of a single generic lineage. Each is rather restricted temporally: *Elphidotarsius* has been found only in Torrejonian beds, *Carpodaptes* is known chiefly from Tiffanian strata, and *Carpolestes* occurs in "Clarkforkian" and earliest Wasatchian deposits.

The nature and extent of similarities between

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carpolestids and plesiadapids indicates that the two families are closely related through a common ancestor.

INTRODUCTION

The radiation of primates in the Paleocene was one of the most successful episodes in the early evolution of eutherians. In North America, members of this initial deployment, particularly plesiadapids, became common or even dominant forms in many local faunas. Other "archaic prosimians" included in this first major radiation of lower primates were the Paromomyidae (including *Phenacolemur*), the Carpolestidae, and, according to some authors, the Picrodontidae and the Microsyopidae. (Recent attempts [e.g. Cartmill, 1972; Martin, 1968] to banish the "archaic prosimians" from the Primates or to transfer them to the Insectivora are unjustified when available evidence is considered *in toto*.)

Renewed interest has focused on these early primates in recent years, resulting in a few broad reviews (e.g. Simons, 1963, 1972; McKenna, 1966; Szalay, 1968a, 1972b). There have also appeared several more specific works that have contributed significantly to our understanding of Paleocene primates (e.g. Simpson, 1955; D. E. Russell, 1959, 1964; Szalay, 1968b, 1969a, 1969b, 1972a; Gazin, 1971; Butler, 1973; Gingerich, in press; and Bown and Gingerich, 1972, 1973). One outcome of the current crescendo of interest in early primates has been the realization of their great diversity, and also of the presence of features in common which unite them more or less closely as members of the Primates. The relationships of these early forms to primates of Eocene or later time have been a subject of investigation. It has long been known that Paleocene *Plesiadapis* and *Phenacolemur* gave rise to Eocene species of the same genera. Recent evidence has strengthened the possibility that some other Paleocene primates may also have had Eocene descendants, e.g. *Plesiolestes* is a plausible ancestor for some Eocene microsyopids (Bown and Gingerich, 1972, 1973).

The interrelationships of the Paleocene primate families and genera are still not fully understood, but a relatively clear picture of affinities and evolutionary trends can be reconstructed in some cases. One family for which this is now possible, the Carpolestidae, forms the subject of this paper. This aberrant group comprises three genera that have been found in deposits of Middle Paleocene to earliest Eocene age in western North America. The three genera, *Elphidotarsius, Carpodaptes*, and *Carpolestes*, constitute a well-documented time-transgressive structural sequence.

The Carpolestidae are known solely from dentitions and gnathic and cranial fragments; unfortunately, no postcranial elements can be confidently referred to the family. Such evidence as has been available has suggested close ties between the Plesiadapidae and the Carpolestidae, but a number of peculiar features clearly segregate the latter at the family level from all other early primates. The most conspicuous feature (and also the most significant taxonomically) is the specialized lower fourth premolar. Through time this tooth became progressively enlarged, multicusped, and bladelike. Concomitant with this development was the reduction of the anterior dentition, except for the large, procumbent medial incisor, which remained prominent in size throughout the lineage. This particular combination of features in the mandibular dentition has evolved independently in several unrelated mammalian groups and has been termed the "plagiaulacoid dentition" (Abel, 1931; Simpson, 1933; also see below, p. 51). As hypertrophy of P_4 proceeded in carpolestids, there was corresponding enlargement of the upper third and fourth premolars (which occlude with P_4). P^3 and P^4 lengthened anteroposteriorly and developed three longitudinal crests bearing cuspules, somewhat resembling upper molars in multituberculates. (In fact, the first discovered

upper premolar of a carpolestid was mistaken for a tooth of a multituberculate.) These features have been and still are regarded as diagnostic of the family Carpolestidae.

Since the discovery of the first carpolestid specimen about half a century ago, only a small number of articles on carpolestids have appeared, and most have been descriptions of new taxa. By 1970, only about twenty specimens had been described or figured in the literature, but large numbers of specimens had been recovered which remained unpublished. Persistent field work in Paleocene deposits has produced sizable samples of these specialized early primates (the largest single species sample from one site is greater than 60 specimens). More than 300 specimens are now known, many of which reveal information previously unknown. The most extensive collections have been recovered for Princeton University by field operations under the direction of Professor G. L. Jepsen; these investigations have been undertaken in the Bighorn Basin for more than forty years. Only three carpolestid specimens discovered by the earliest of these expeditions have been described previously (Jepsen, 1930). The extensive Princeton collection, as well as numerous other new specimens, provide ample carpolestid material to serve as the basis for a systematic revision. In addition, better preserved specimens and samples of larger size can now contribute significantly to our understanding of carpolestids and their role in the initial radiation of the Primates.

ABBREVIATIONS

AMNH — American Museum of Natural History, New York
CM — Carnegie Museum, Pittsburgh
MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
PU — Princeton University Museum, Princeton, New Jersey
ROM — Royal Ontario Museum, Toronto, Ontario
UA — University of Alberta, Edmonton
UKMNH — University of Kansas Museum of Natural History, Lawrence
UMMP — University of Michigan Museum of Paleontology, Ann Arbor
UMVP — University of Minnesota, Minneapolis
USNM — United States National Museum, Washington, D.C.
UW — University of Wyoming, Laramie
YPM — Peabody Museum of Natural History, Yale University, New Haven, Connecticut
B — Breadth
L — Length
MD — Mandibular depth, measured on the buccal side beneath the anterior root of M_1.
N — Number of observations (specimens)
OR — Observed range
s — Standard deviation
V — Coefficient of variation
$\bar{X}$ — Mean

Dental terminology used in this study is that of Szalay (1969a). Dimensions of the cheek teeth and depth of the mandible have been measured in the manner illustrated in Figure 1, using an ocular micrometer fitted to a lens of a binocular microscope.

HISTORY OF STUDY

The first carpolestid described was *Carpodaptes aulacodon* Matthew and Granger (1921). The generic name means "fruit eater"; the specific name alludes to the vertical grooves on the lower fourth premolar, a condition similar to that of P_4 in plagiaulacoid multituberculates and certain marsupials. The species was based solely on the type specimen and, in the absence of any comparable species, Matthew and Granger were duly reluctant to suggest its

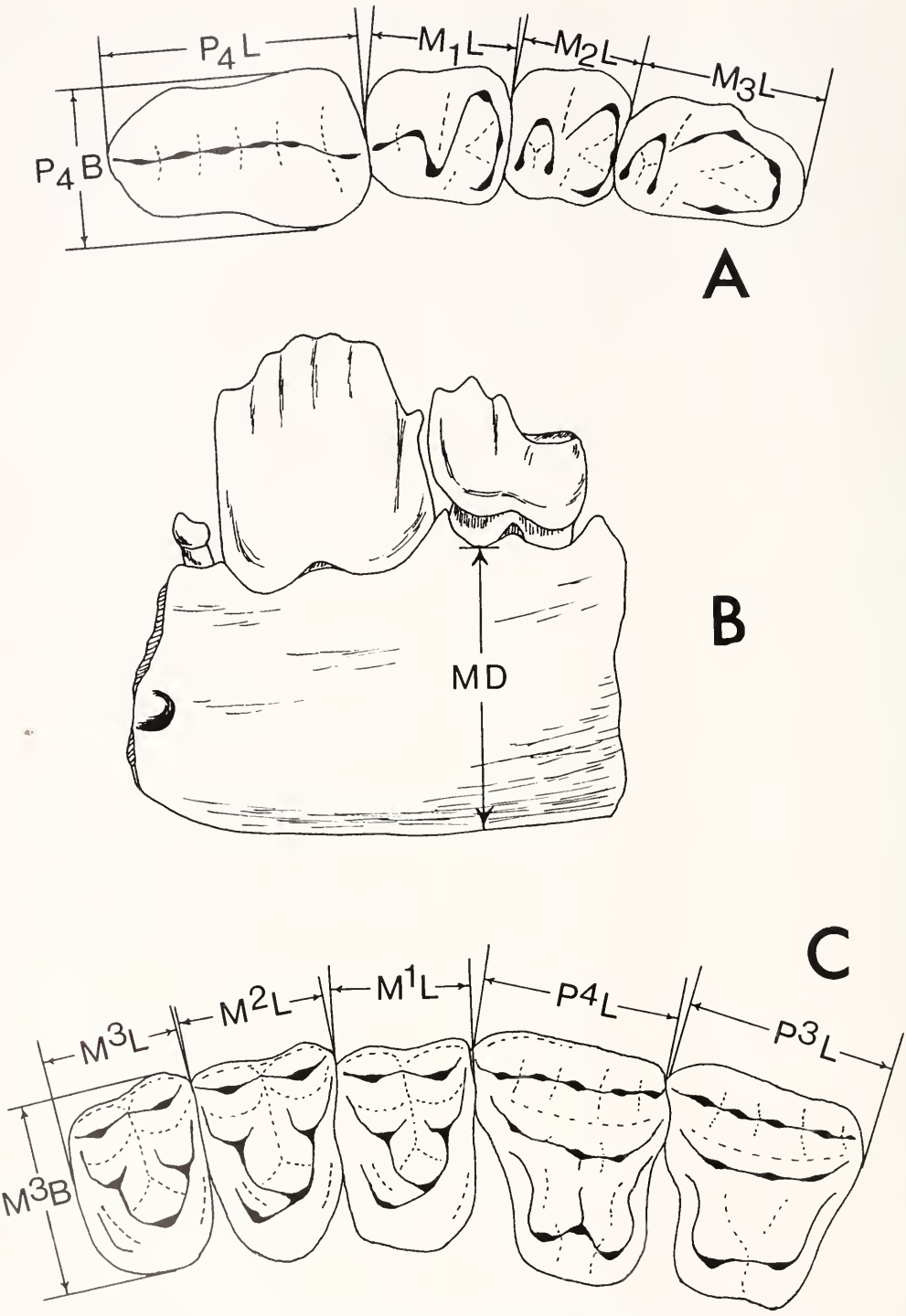


Figure 1. Schematic drawings to demonstrate method of taking measurements. All dimensions are in millimeters. A) crown view of P_4–M_3. L = maximum mesiodistal length, as shown. Breadths (B) are maximum dimensions measured perpendicular to length. B) lateral view of mandible. MD = mandibular depth beneath anterior root of M_1. C) crown view of P^3–M^3.

affinities. They speculated only that "it may be a primate, a menotyphlan insectivore, or neither" (Matthew and Granger, 1921:6).

J. W. Gidley (1923) proposed *Elphidotarsius florencae* for a mandibular fragment preserving P_4 through M_3. Again the holotype was the only known specimen. He noted resemblances of the molars to those of fossil tarsioids such as *Tetonius,* therefore placing *Elphidotarsius* provisionally in the Tarsiidae, the name then applied to many Paleocene and Eocene primates. He did not compare the specimen to *Carpodaptes.*

Carpolestes ("fruit stealer") was named by Simpson (1928) to accommodate the new species *Carpolestes nigridens* from the Eagle Coal Mine at Bear Creek, Montana. Simpson regarded *Carpolestes* as a close relative of *Carpodaptes,* classifying both as aberrant members of the Tarsiidae. The following year he described a second species from Bear Creek, *Carpolestes aquilae* (Simpson, 1929).

Jepsen (1930) named a third species of *Carpolestes, C. dubius.* Included in his hypodigm was a maxilla with four teeth, the first upper dentition of a carpolestid to be identified. Jepsen recognized that the type and only known specimen of the supposed multituberculate *Litotherium complicatum* (Simpson, 1929), an isolated upper premolar from Bear Creek, was actually P^3 of *Carpolestes.* (This eliminated the Multituberculata from the known fauna of Bear Creek.) Like Matthew and Granger, he deferred definite ordinal assignment for *Carpolestes,* stating, "It is possible to select suites of characters which, taken by themselves, would place *Carpolestes* in any one of several orders," (Jepsen, 1930:523).

The relationship of *Elphidotarsius* to *Carpodaptes* and *Carpolestes* was recognized by Simpson (1935b), who proposed the family Carpolestidae for the reception of the three genera. He also noted adaptive features shared by this family, the Plesiadapidae, and the Apatemyidae. As diagnostic characters of the Carpolestidae, Simpson listed the enlarged lower fourth premolar and the procumbent enlarged lower incisor. The dental formula remained controversial, however. Jepsen (1930) had proposed the mandibular dental formula 1.0.4.3, regarding the tooth immediately behind the enlarged incisor as P_1. Simpson (1935b:10), although conceding that it was "impossible to determine whether the following tooth is a canine or P_1", considered it "slightly more probable that it is the canine". Discussing the degree of relationship among the three genera, Simpson (1937b:161) remarked that the morphologic sequence *Elphidotarsius-Carpodaptes-Carpolestes* "may be a direct phylogeny, although the possible age difference between the last two genera seems too small to permit such a marked structural advance in a direct descendant, and it is more likely that some collateral evolution is involved".

In 1936, Simpson described *Carpodaptes hazelae* from the Scarritt Quarry in the Crazy Mountain Field of Montana. The next year, he described the most complete known upper dentition of a carpolestid (referable also to *C. hazelae*), preserving three molars and four antemolar teeth. The most anterior tooth unfortunately has been lost since Simpson's description, and it is not preserved in any carpolestid found subsequently. In the same paper, Simpson (1937a) reasserted his view that carpolestids represent early aberrant primates and again stressed the resemblances to *Plesiadapis,* concluding that these similarities could only indicate close affinity and common ancestry.

Dorr's field work in the Hoback Basin of western Wyoming yielded a Tiffanian fauna which included a previously unknown carpolestid, *Carpodaptes hobackensis* (Dorr, 1952). Dorr suggested that this species might be more nearly intermediate between *Elphidotarsius* and *Carpolestes* than either other named species of *Carpodaptes.*

Gazin (1956b) reported the occurrence of *Carpolestes,* cf. *C. dubius,* in latest Paleo-

cene beds near Buckman Hollow, southwestern Wyoming, the only record of a carpolestid in the southern part of the Green River Basin.

The Carpolestidae were regarded as strictly North American until the description of *Saxonella*, from Walbeck, Germany, by D. E. Russell (1964). Due to several significant differences between the North American carpolestids and the new European form, Russell was obliged to redefine the family in order to include *Saxonella*, and to create two subfamilies, the Carpolestinae (for the three North American genera) and the Saxonellinae (for *Saxonella*). This classification was adopted by some subsequent authors (e.g. Romer, 1966; McKenna, 1967). Nevertheless, *Saxonella* seems to have as much or more in common with plesiadapids. Some similarities were mentioned by Russell (1964). Szalay (1968a, 1969a) reiterated the resemblances and intimated a relationship between *Saxonella* and the Plesiadapidae. Van Valen (1969) went a step further and formally placed the Saxonellinae in the Plesiadapidae. He grouped Carpolestidae with the Paromomyidae, Microsyopidae, Plesiadapidae, and Picrodontidae in a new superfamily, the Microsyopoidea.

The first carpolestids from the Paleocene of Canada were reported by L. S. Russell (1967). He referred three fragmentary specimens from Alberta to a new species, *Carpolestes cygneus*. As noted by Krishtalka (1973), however, this species is clearly referable to *Carpodaptes*. Krishtalka described additional specimens of *Carpodaptes* from Canada, this time from the Cypress Hills of southeastern Alberta.

Both *Carpodaptes* and a new species of *Elphidotarsius*, *E. shotgunensis*, were recorded in the Shotgun Local Fauna of western Wyoming (Gazin, 1971). The association of two different genera of carpolestids is otherwise unknown.

Szalay (1972b) suggested that the genus *Carpolestes* should probably be regarded as a synonym of *Carpodaptes* (a view depicted in a chart by Szalay earlier [1969a: fig. 27], but not mentioned in the text of that paper). He also proposed a new interpretation of the dental formulae of carpolestids. In analogy with his interpretation of the formula in *Pronothodectes* and in Middle Paleocene paromomyids, he suggested the formula $\frac{2.1.3.3}{2.1.3.3}$ or *Elphidotarsius*, and the same formula, except for the loss of P_2, for *Carpodaptes* and *Carpolestes*. He also figured a tooth as the first known upper incisor of a carpolestid (Szalay, 1972b: fig. 1–9).

Other notable discussions of the Carpolestidae not cited above include those of Abel (1931), Simpson (1940), Hill (1953), Saban (1961), and Simons (1963, 1972).

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE

Carpolestids have been discovered in beds of Middle Paleocene (Torrejonian) to earliest Eocene (Wasatchian) age in the Rocky Mountain region of western North America (see Fig. 2). Where different genera have been found in the same depositional basin, they occur in stratigraphic succession, *Elphidotarsius* below *Carpodaptes* (except in the Shotgun Local Fauna), and *Carpodaptes* below *Carpolestes*. The temporal range of each genus appears to be rather strictly limited, suggesting that carpolestids may be of value in determining the approximate ages of faunas. *Elphidotarsius* is known only in beds of Torrejonian age. Its latest known occurrence is in the late Torrejonian Shotgun Local Fauna, where it is associated with the earliest known *Carpodaptes*. All other records of *Carpodaptes* are restricted to the Tiffanian (Late Paleocene). *Carpolestes* first appears in the Silver Coulee beds of the northern Bighorn Basin (Princeton Quarry level) and is known from several sites regarded as "Clarkforkian" (latest Paleocene) in age, as well as a few of Early Eocene age.

Only at Shotgun do two carpolestid species occur together. The Shotgun Local Fauna is diverse, and the sample is very large but consists predominantly of isolated teeth. Included in the fauna are other pairs of related genera rarely or never found together elsewhere. There has been some question as to the age of the Shotgun fauna and, in fact, whether the entire assemblage is the same age. Some forms suggest a late Torrejonian age while others are more indicative of the Tiffanian. Patterson and McGrew (1962) believed that the fauna indicated an early Tiffanian age, but more recently they (personal communication, 1973) and C. B. Wood (personal communication) regard the age as late Torrejonian.

The primates, described by Gazin (1971), include *Palaechthon, Palenochtha, Plesiolestes, Paromomys,* and *Elphidotarsius* (all recorded only from Torrejonian deposits), *Pronothodectes* (usually from the Torrejonian but known also from the early Tiffanian [Gazin, 1956a]), and *Phenacolemur, Plesiadapis,* and *Carpodaptes* (all typically Tiffanian or later in age). From the progressive nature of some species of the Torrejonian genera, Gazin (1971) inferred a late Torrejonian age for the Shotgun assemblage (as he had earlier, [Gazin, 1961]), but he conceded that the presence of the three genera otherwise unknown in pre-Tiffanian faunas[1] "might suggest a mixture of materials from different levels" (Gazin, 1971:15).

The latter hypothesis is more compatible with the primate evidence, particularly the carpolestids. Specimens of *Carpodaptes* from Shotgun bear closest resemblance to those from Cedar Point Quarry (definitely of Tiffanian age) and, as noted above, *Carpodaptes* has not been found at any other pre-Tiffanian site. But aside from the primates, the fauna is overwhelmingly Torrejonian in aspect, with few Tiffanian forms; the reverse would be expected in a Tiffanian deposit containing reworked Torrejonian fossils. Resolution of this problem is, however, beyond the scope of this paper, and herein the age of the Shotgun Local Fauna is accepted as late Torrejonian.

The uniqueness of the Shotgun fauna may be due in part to its unusual paleoenvironment. In late Paleocene time, the site was flanked on the east by the extensive, probably saline Waltman Lake, which was connected at least intermittently to the Cannonball Sea (McGrew, 1963). Similar paleoecological conditions have not been sampled elsewhere in the North American Paleocene.

Mention should also be made of the "Clarkforkian" problem. The use of this term, proposed by H. E. Wood, et al., (1941), has met some opposition in recent years. For example, R. C. Wood (1967), who reviewed the Clark Fork fauna and stratigraphy, concluded that available evidence "scarcely warrants recognition of the Clark Fork as a provincial age, faunal zone, or member of the Polecat Bench Formation" (Wood, 1967:28). Nevertheless, field work in the type Clark Fork area and in other Late Paleocene deposits in recent years has yielded considerable new evidence suggesting that the term "Clarkforkian" may be valid and useful as a North American Land Mammal "Age" (D. C. Parris, R. E. Sloan, personal communication). The genus *Carpolestes* has been regarded as characteristic of the "Clarkforkian" (Sloan, 1969: fig. 5) and is one of several forms whose overlapping temporal ranges may be used in a redefinition of the "Clarkforkian" (Sloan, *in litt.,* 5/22/73). Sloan (1969) placed Princeton Quarry just below the Tiffanian–"Clarkforkian" boundary; more recently he suggests that it is approximately at the boundary (Sloan, personal communication, 6/28/73). He regarded Olive, Bear

[1] The only purported Torrejonian record of *Plesiadapis* is in the Battle Mountain Local Fauna of the Hoback Basin, first considered of Torrejonian age (Dorr, 1958), but now regarded as early Tiffanian (Gingerich, personal communication).

Creek, and Buckman Hollow to be within the "Clarkforkian" (Sloan, 1969). Except for the Olive Local Fauna, here considered Tiffanian, I have adopted Sloan's view and regard the Princeton Quarry level as earliest "Clarkforkian". Pending a revised definition of the "age" (Sloan and Parris, in preparation), the name "Clarkforkian" appears herein in quotation marks.

To date, more than 300 carpolestid specimens (mostly jaws) have been collected (*Elphidotarsius*: 30+; *Carpodaptes*: 200+;

Carpolestes: 80+). They are among the commonest mammals at many Middle and Late Paleocene sites, and one may infer that they were not uncommon members of the biocoenose. For example, in the Polecat Bench sequence, more than 20 jaws of *Elphidotarsius* are included in the collection from Rock Bench Quarry, and more than 60 jaws of *Carpodaptes* have been recovered at Cedar Point Quarry, making it

←

Figure 2. Map of localities where carpolestids have been found.

Locality	*Age*	*Formation*	*Occurrence*	*Reference to locality or to carpolestid record*
1) Swan Hills	Late Paleocene (Tiffanian)	Paskapoo	*Carpodaptes cygneus*	L. S. Russell, 1967
2) Cypress Hills	Late Paleocene (Tiffanian)	Ravenscrag	*Carpodaptes*, cf. *C. cygneus*	Krishtalka, 1973
3) near Roche Percee	Late Paleocene (Tiffanian)	Ravenscrag	*Carpodaptes cygneus*	Krause, personal communication
4) Crazy Mountain Field				
a) Gidley Quarry	Middle Paleocene (Torrejonian)	Fort Union (Lebo Member)	*Elphidotarsius florencae*	Gidley, 1923; Simpson, 1937b
b) Scarritt Quarry	Late Paleocene (Tiffanian)	Fort Union (Melville Member)	*Carpodaptes hazelae*	Simpson, 1936
c) Princeton Loc. 11	Late Paleocene (Tiffanian)	Fort Union	*Carpodaptes* sp.	Simpson, 1937b
5) Eagle Coal Mine at Bear Creek	Late Paleocene ("Clarkforkian")	Fort Union	*Carpolestes nigridens*	Simpson, 1928, 1929
6) Circle	Late Paleocene (Tiffanian)	Tongue River	*Carpodaptes*, cf. *C. hazelae*	Sloan, *in* D. E. Russell, 1967
7) Olive	Late Paleocene (Tiffanian)	Tongue River	*Carpodaptes* sp.	Sloan, *in* D. E. Russell, 1967
8) Medicine Rocks Site 1 near Ekalaka	Middle Paleocene (Torrejonian)	Tongue River	*Elphidotarsius*, cf. *E. florencae*	Princeton University site, unpublished
9) Judson	Late Paleocene (Tiffanian)	Tongue River	*Carpodaptes*, poss. *C. cygneus*	Holtzman and Sloan, personal communication
10) Polecat Bench region				Princeton University sites, in Jepsen, 1930, or unpublished
a) Rock Bench Quarry	Middle Paleocene (Torrejonian)	Polecat Bench	*Elphidotarsius*, cf. *E. florencae*	
b) Long Draw Quarry (Carbon Co., Montana)	Late Paleocene (latest Tiffanian)	Polecat Bench	*Carpodaptes jepseni* ?	
c) Silver Coulee beds: Princeton, Schaff, Fritz, and Storm Quarries	Late Paleocene (Tiffanian-"Clarkforkian" boundary)	Polecat Bench	*Carpolestes dubius*	
d) Paint Creek	Paleocene-Eocene boundary	Willwood	*Carpolestes nigridens*	
e) Twisty-turn Hollow	earliest Eocene (Wasatchian)	Willwood	*Carpolestes* sp.	
11) Big Horn County				Princeton University sites
a) Cedar Point Quarry	Late Paleocene (Tiffanian)	Polecat Bench	*Carpodaptes hazelae*	
b) Divide Quarry	Late Paleocene (latest Tiffanian)	Polecat Bench	*Carpodaptes jepseni*	
c) Cleopatra Reservoir site	Late Paleocene ("Clarkforkian")	Polecat Bench	*Carpolestes* sp.	
12) Togwotee Pass	Late Paleocene ("Clarkforkian" or Paleocene-Eocene boundary)	"lower variegated sequence"	*Carpolestes* sp.	McKenna, 1972
13) Dell Creek	Late Paleocene (Tiffanian)	Hoback	*Carpodaptes hobackensis*	Dorr, 1952
14) Shotgun	Middle Paleocene (latest Torrejonian)	Fort Union (Shotgun Member)	*Elphidotarsius shotgunensis* and *Carpodaptes*, cf. *C. hazelae*	Gazin, 1971
15) Badwater, "Malcolm's Locality"	Late Paleocene (Tiffanian)	Fort Union (Shotgun Member)	*Carpodaptes* sp.	Krishtalka, personal communication; Black and Dawson, 1966
16) Buckman Hollow	Late Paleocene ("Clarkforkian")	Wasatch (Chappo Member)	*Carpolestes* sp.	Gazin, 1956b
17) Mason Pocket at Tiffany	Late Paleocene (Tiffanian)	Tiffany	*Carpodaptes aulacodon*	Matthew and Granger, 1921; Simpson, 1935b

second in abundance to *Plesiadapis* at this productive site. On the other hand, carpolestids are decidedly less common at some localities, such as the Crazy Mountain Field, where only 11 specimens of *Carpodaptes* are known from Scarritt Quarry, and only a single jaw of *Elphidotarsius* has been recorded among 382 identifiable mammalian jaws from Gidley Quarry (Simpson, 1937b:34). Nevertheless, the wide geographic distribution and often common occurrence of carpolestids contribute to their utility in correlating Paleocene faunas.

SYSTEMATIC REVISION

Maglio (1971:372) recently stated:

> " . . . the goal of the paleo-biologist . . . is not the recognition of fossil "taxa" and the establishment of a formal terminology for ever smaller segments of a phyletic continuum. On the contrary, it is the establishment of evolutionary units that can be traced through long periods of time and with which broad evolutionary phenomena can be studied."

I concur with this view. Systematics should be a means for better understanding animals and their evolution; it should not be an end in itself. The systematic revision presented here has been approached with this in mind. Synonymy of named species has been proposed only when there can be little doubt that the taxa involved are conspecific. Closely similar established species have been retained when any consistent distinctions could be discerned. New species have not been proposed unless specimens were demonstrably different from existing species. I believe that this somewhat conservative approach will promote a clearer understanding of the evolution and interrelationships of the Carpolestidae.

Order **PRIMATES** Linnaeus, 1758

Infraorder **PLESIADAPIFORMES** Simons, 1972[1]

Superfamily PLESIADAPOIDEA Trouessart, 1897

Family CARPOLESTIDAE Simpson, 1935

Carpolestidae Simpson, 1935b: 9.

Type Genus: *Carpolestes* Simpson, 1928.
Included Genera: *Carpodaptes, Elphidotarsius,* and *Carpolestes.*

Distribution: Middle Paleocene (Torrejonian) to Early Eocene (early Wasatchian) of western North America (Alberta, Saskatchewan, Montana, North Dakota, Wyoming, and Colorado).

Emended diagnosis: Very small aberrant primates. Dental formula $\frac{?2.?1.?3.3}{2.1.2\text{–}3.3}$. Mandibular dentition characterized by enlarged, rooted, anteriorly inclined medial incisor, followed by greatly reduced tooth (lateral incisor). Root of enlarged incisor implanted at about 45° angle to vertical and extending back no further than to a point beneath P_3. Canine present but also much reduced. P_1 absent; P_2 either very small and button-like (*Elphidotarsius*) or lost (*Carpodaptes and Carpolestes*). P_3 small, double-rooted (*Elphidotarsius*), or single-rooted (*Carpodaptes* and *Carpolestes*). P_4 enlarged (relatively more so in later forms), specialized into polycuspate, trenchant blade; talonid heel small, consisting of one cusp, distinct in *Elphidotarsius* and *Carpodaptes,* becoming merged with blade in *Carpolestes.* Proliferation of apical cusps on P_4 occurring in later forms. Molars, except M_1, deviating little from generalized plesiadapid pattern. Trigonid of M_1 longer anteroposteriorly than in M_2 or M_3; widely splayed in *Carpodaptes* and *Carpolestes,* with paraconid directly anterior to protoconid, forming continuation of P_4 blade. Metaconid of M_1 always posterolingual to

[1] This name first appeared in Simons (1972) but was credited to "Simons and Tattersall, 1972", a work which has not been published.

protoconid. Molar talonids broad, basined, with distinct hypoconid and entoconid, small or indistinct hypoconulid (except on M_3). Talonid of M_1 smaller, more compressed anteroposteriorly than in M_2. M_3 not reduced, with pronounced third lobe bearing two cusps (twinned hypoconulid). P_4 (particularly) and molars exodaenodont. Mandible shallowest in *Elphidotarsius*, deepest in *Carpolestes*.

At least 2 incisors and small canine (?) present in upper jaw. P^2 small, single-rooted, bearing one main cusp. P^{3-4} either of plesiadapid type, smaller than molars, relatively unspecialized (*Elphidotarsius*), or greatly modified, larger than molars, polycuspate with 3 longitudinal rows of cusps (*Carpodaptes* and *Carpolestes*). Upper molars with primitive plesiadapid morphology; hypocone small but distinct on M^{1-2}, less distinct or represented by shelf on M^3.

Discussion: The Carpolestidae were a rapidly evolving group of archaic primates in which extreme specializations of P_4 and P^{3-4} were achieved. The three known genera constitute a sequence that, in general, shows enlargement and specialization through time; they are almost surely in a single lineage. The earliest genus, *Elphidotarsius*, is relatively unspecialized and easily derivable from a form morphologically close to the earliest plesiadapids; it contrasts with *Carpolestes*, in which the family traits are fully manifested.

Teeth in which the base of the crown extends laterally well beyond the roots have been described as "exodaenodont". The condition was first observed in dimylid insectivores (Hürzeler, 1944; Saban, 1958) and later noted in picrodontids and some bats (McGrew and Patterson, 1962). It is especially conspicuous in the lower cheek teeth, particularly P_4, of carpolestids. Both Hürzeler and Saban suggested that it correlates with malacophagy, but this seems to have little basis. A molluscan diet is very unlikely for picrodontids and bats (as pointed out by McGrew and Patterson, 1962:6), and equally improbable for carpolestids.

The dental formula in carpolestids has been controversial. The interpretation I present differs from that of most previous authors (e.g., Matthew and Granger, 1921; Jepsen, 1930; Simpson, 1935b, 1937b; Dorr, 1952; Hill, 1953; Saban, 1961; and Simons, 1972) and is in accord with that recently proposed by Szalay (1972b). (Justification of the new formula is presented below.)

The upper dental formula is necessarily uncertain, since anterior teeth are known only in the most advanced form, *Carpolestes*, and even in that genus only roots are preserved. If the antemolar teeth are correctly interpreted, there were two incisors, a canine, and three premolars.

Elphidotarsius Gidley, 1923

Elphidotarsius Gidley, 1923: 10; Simpson, 1937b: 162.

Type Species: *Elphidotarsius florencae* Gidley, 1923.

Included Species: *E. florencae* and *E. shotgunensis*.

Distribution: Middle Paleocene (Torrejonian) of Wyoming and Montana.

Emended Diagnosis: Small, relatively unspecialized carpolestids. Lower dental formula 2.1.3.3. Medial incisor (I_1?) enlarged and procumbent; crown lanceolate in outline; root extending back to a point approximately below canine. Lateral incisor (I_2?) and canine known only from alveoli. Alveolus of P_2 very small, smaller than those of ?I_2 and P_3, and situated slightly lingual to them. P_3 premolariform, larger relatively and absolutely than in *Carpodaptes* and *Carpolestes;* crown with prominent apical cusp preceded by lower, less distinct cuspule, and followed by low but distinct heel; two roots, partially fused, occupying a single alveolus. P_4 enlarged (larger than M_1), bladelike, bearing 4 longitudinally arranged apical cusps followed by lower but well defined talonid cusp. M_1

with anteroposteriorly extended trigonid, paraconid and metaconid lingual to protoconid, the metaconid the more lingual of the two. Talonid of M_1 with distinct hypoconid and entoconid. Trigonids of M_2 and M_3 anteroposteriorly compressed. Upper dentition anterior to P^3 unknown. P^3-M^3 all broader (buccolingually) than long. P^3 distinctly smaller than P^4, with prominent lingual cusp and major buccal cusp, the latter followed by a smaller buccal cusp. P^4 about same size as M^1, more triangular, longer buccally, shorter lingually; moderately specialized with buccal row of 4 cusps, median anteroposterior crest bearing large central cusp, and pronounced lingual cusp directly internal to the latter; incipient hypocone at internal end of posterolingual cingulum. Hypocone of molars formed as in P^4, small, but more distinct than in P^4, connected to protocone by "nannopithex fold". Pronounced ectocingulum and anterolingual and posterolingual cingula on M^{1-3}, weaker on P^{3-4}; cingula not continuous onto lingual face of teeth.

Elphidotarsius florencae Gidley, 1923
Figures 3, 4

Elphidotarsius florencae Gidley, 1923: 10; Simpson, 1937b: 163.

Holotype: USNM 9411, left mandible with P_4-M_3.

Hypodigm: type specimen only.

Horizon and Locality: Middle Paleocene (Torrejonian), Lebo Member, Fort Union Formation: Gidley Quarry, Crazy Mountain Field, Montana.

Emended Diagnosis: Less progressive and slightly smaller than *E. shotgunensis*. P_4 and M_1 shorter anteroposteriorly but broader buccolingually than in *E. shotgunensis*. Lower molars as long as, or longer than, broad. Trigonid of M_1 more anteroposteriorly extended (i.e., paraconid and metaconid more widely separated) than in M_2 or M_3, but less so than in *E. shotgunensis*.

Discussion: Simpson's (1937b) thorough discussion precludes the need for redescription of the holotype. The recently described species *E. shotgunensis* (Gazin, 1971), permits a more precise definition of *E. florencae*. Unfortunately, since only one specimen is known, information on intraspecific variability is unavailable, unless the sample described below, *Elphidotarsius* sp., cf. *E. florencae*, is definitely referable to it.

Figure 3. *Elphidotarsius florencae* Gidley, holotype, USNM 9411, left P_4–M_3. Crown view (above) and lateral view (below). × 6.

Elphidotarsius sp., cf. *E. florencae* Gidley
Figures 4B, 5A, 6–8, 34A, 34B

The largest sample of a population of *Elphidotarsius* is from the Middle Paleo-

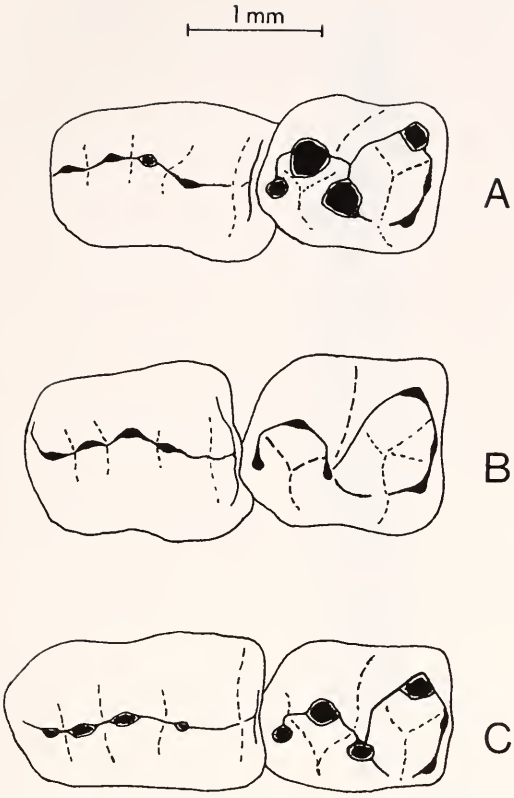


Figure 4. Crown view of right P_4–M_1 of *Elphidotarsius*, to same scale. A) *E. florencae*, holotype, USNM 9411, from Gidley Quarry. B) *E.*, cf. *E. florencae*, PU 14792, from Rock Bench Quarry. C) *E. shotgunensis*, holotype, AMNH 88311.

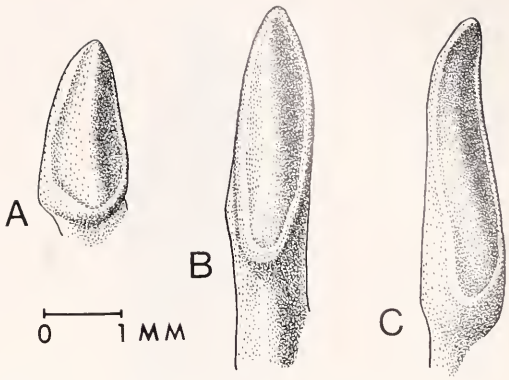


Figure 5. Lower left medial incisors of carpolestids. A) *Elphidotarsius*, cf. *E. florencae*, PU 14282. B) ?*Carpodaptes* sp., UW 6530 (reversed). C) *Carpolestes dubius*, PU 14235.

cene (Torrejonian) Rock Bench Quarry, Polecat Bench Formation of Park County, Wyoming. The more than twenty specimens are closely comparable to the holotype of *E. florencae*. There are no significant morphologic differences, but the individuals in the Rock Bench sample are, in general, slightly larger than the holotype. A Student's t-test comparing the dimensions of the type with those of the Rock Bench specimens yielded inconclusive results, neither favoring erection of a new species nor declaring the two samples positively conspecific.

Description: The Rock Bench Quarry sample includes many specimens that provide new information about *Elphidotarsius*. A few reveal the anterior part of the mandible and suggest the dental formula 2.1.3.3. The Torrejonian plesiadapid *Pronothodectes*, which is close to *Elphidotarsius* in many features (see below), has a similar dental pattern and the formula 2.1.3.3. (e.g., PU 14783; Szalay, 1972b; Gingerich, personal communication). Analogy with *Pronothodectes* strengthens the interpretation of the lower dental formula of *Elphidotarsius* adopted here.

The enlarged medial incisor is preserved in one specimen, PU 14282 (Figs. 5A and 6). It is lanceolate in outline and quite broad at the base, much broader than in either of the other carpolestid genera. The dorsal (lingual) surface is broad and slightly convex, bounded laterally by a ridge running from the tip to the base of the crown, where it merges with a prominent internal cingulum. The incisor, although shorter, somewhat resembles that of *Plesiolestes*. A small basal cusp arising from the internal cingulum is found in *Pronothodectes* and *Plesiadapis*, but is conspicuously absent from the incisor of *Elphidotarsius*. An interstitial facet is present in PU 14282, but there is no occlusal facet such as observed in *Plesiadapis* by Gingerich (in press).

Figure 6. *Elphidotarsius*, cf. *E. florencae* Gidley, PU 14282, left dentary with medial incisor, P_4–M_3. Crown view (above) and lateral view (below). × 6. Rock Bench Quarry.

Three alveoli are present between the enlarged incisor and P_3. They are interpreted to have held I_2, C, and P_2. The alveolus just behind the medial incisor is mesiodistally compressed and slightly larger than that for the canine. Its slight anterior inclination suggests that I_2 was somewhat procumbent. The second alveolus is slightly

Figure 7. *Elphidotarsius*, cf. *E. florencae* Gidley, PU 14791, right dentary with P_3–M_3. Crown view (above) and lateral view (below). × 6. Rock Bench Quarry.

larger than that of P_2, supporting the view that it held the canine. The socket for P_2 is situated just lingual to those of the canine and P_3. Its diminutive size favors the supposition that P_2 has been lost in *Carpodaptes* and *Carpolestes,* both of which have one less tooth in the mandible.

P_3 in the Rock Bench sample is pre-

molariform and relatively unreduced. Its two roots are partially joined, occupying a single alveolus. The crown bears a well developed central cusp followed by a low, well differentiated talonid cusp. A short anterior shelf rises in a tiny, low cusp, anterior to the main cusp.

P_4 and the lower molars are very similar to those in the type of *E. florencae*. In some individuals, the cheek teeth (P_4-M_3) are relatively broader buccolingually than in the type. M_2, particularly, is almost always as broad as it is long (as in the type), and often is broader than long. Nevertheless, the extent of variation observed in the Rock Bench sample and in other large samples of carpolestids indicates that this feature is not of taxonomic importance.

P_4 in the Rock Bench sample bears four apical cusps and a lower, pronounced talonid cusp, but it is comparable in length to *E. florencae* and shorter than in *E. shotgunensis*. The third apical cusp is the largest and highest and is probably homologous with the protoconid. (This cusp in the type of *E. florencae* shows apical wear, thus appearing lower than the cusp anterior to it.) Just behind, lower, and slightly lingual to the third cusp is a cusp probably homologous with the metaconid. The second cusp appears to be the homologue of the paraconid and is nearly as prominent as the protoconid. Anterior to it is an accessory cusp, the lowest and least developed of the four. Butler (1973) has also suggested these homologies.

As in the holotype of *E. florencae*, M_1 is relatively generalized. The trigonid is only slightly splayed (less anteroposteriorly extended than in *E. shotgunensis*) but is more buccolingually compressed than in M_2 and M_3. The paraconid of M_1 is usually the weakest trigonid cusp, while the protoconid is the largest. In M_2 and M_3, the metaconid is usually the highest trigonid cusp and the paraconid remains small and low.

The mandible in *Elphidotarsius* is shallower than in *Carpodaptes* or *Carpolestes*.

Two specimens in the Rock Bench sample (PU Nos. 17439 and 17736) reveal the upper cheek teeth of *Elphidotarsius*. The better of these, PU 17439, is a right maxillary fragment with P^3-M^3 and two alveoli anterior to P^3 (Figs. 8, 34B). Each of the anterior alveoli held a single-rooted tooth, P^2, and C or possibly P^1. The latter was the smallest of the known upper teeth. P^3 and P^4 reveal new evidence pertinent to the origin and affinities of the Carpolestidae. They are unspecialized relative to their development in *Carpodaptes* and *Carpolestes*, but compare very closely in structure with P^{3-4} of *Pronothodectes*. The resemblance is striking and is indeed closer between *Elphidotarsius* and *Pronothodectes* than between the former and either of the other carpolestid genera. The similarities involve much of the dentition and are surely indicative of true relationship. They support the conclusion that the Carpolestidae and the Plesiadapidae shared a close common ancestor. It is emphasized, nonetheless, that certain features are present in P^{3-4} of *Elphidotarsius* that clearly foreshadow developments more fully manifested in *Carpodaptes* and *Carpolestes*.

P^3 is substantially smaller than P^4, and the latter and M^1 are subequal. Both P^3 and P^4 are pyriform in outline, considerably longer on the buccal side than lingually. Both are much shorter anteroposteriorly than in the two later genera. P^3 has two buccal cusps, a prominent one about in the center of the buccal crest, and a smaller cusp behind it. A longitudinal crest lies just lingual to the middle of the tooth and bears one central cusp. Internal to this is a lingual shelf, unfortunately fractured anteriorly in the only known specimen, so the possible presence of a cusp there can be neither verified nor ruled out. There is a faint ectocingulum. P^4 is larger and has (as in later carpolestids and *Pronothodectes*) three longitudinal sections (rows of cusps, or crests with one or more cusps). There are four buccal cusps. The most anterior is small, possibly homologous with the parastyle. Behind it, located at approxi-

TABLE 1. METRICAL DATA FOR LOWER CHEEK TEETH OF *ELPHIDOTARSIUS*, CF. *E. FLORENCAE*, FROM ROCK BENCH QUARRY, POLECAT BENCH FORMATION.

		N	OR (mm)	$\bar{x}$	s	V
P_4	length	16	1.7–1.9	1.79 ± .02	.085 ± .015	4.8 ± .8
	breadth	15	1.3–1.6	1.40 ± .03	.107 ± .020	7.6 ± 1.4
M_1	length	15	1.4–1.6	1.50 ± .01	.038 ± .007	2.5 ± .5
	breadth	14	1.3–1.6	1.44 ± .02	.093 ± .018	6.5 ± 1.2
M_2	length	15	1.3–1.6	1.41 ± .02	.083 ± .015	5.9 ± 1.1
	breadth	15	1.4–1.7	1.50 ± .02	.093 ± .017	6.2 ± 1.1
M_3	length	11	1.8–2.1	1.95 ± .02	.082 ± .017	4.2 ± .9
	breadth	10	1.2–1.4	1.29 ± .02	.074 ± .017	5.7 ± 1.3
Mandibular depth		14	2.8–3.5	3.12 ± .05	.197 ± .037	6.3 ± 1.2

mately the center of the crest, is a prominent cusp (paracone?), followed by another well-developed cusp (metacone?). The last cusp on the buccal crest is much smaller and may be homologous with the metastyle. A central, longitudinal, crescentic ridge bears one large cusp anteriorly. Internal to this, a well-expressed cusp rises anteriorly from the lingual cingulum and is followed by a slight rise of enamel, probably an incipient hypocone. There is an ectocingulum, and anterolingual and posterolingual cingula are joined internally by the lingual cingulum.

The upper molars deviate little from the primitive plesiadapid pattern. They are very similar morphologically to the molars in other carpolestids, which have been thoroughly described by previous authors (Jepsen, 1930; Simpson, 1937a). The three trigon cusps are high and prominent; the paraconule and metaconule are smaller but distinct. A cingular hypocone, connected to the protocone by a "nannopithex fold", is well expressed on M^1 and M^2 but is virtually absent from M^3. Pronounced cingula are present on the external, anterior, and posterior borders, except on M^3, where the postcingulum is restricted to the lingual half of the tooth. The molars decrease in size from M^1 to M^3, and in M^3 the posterobuccal corner (metacone area) is greatly reduced. The molars in PU 17439 are more buccolingually distended than in many specimens of other carpolestids.

If the allocation of the Rock Bench Quarry sample to *E. florencae* is correct, speculations can be offered regarding the apparent size discrepancy between specimens in this sample and the holotype. The holotype may represent an unusually small individual, or, more probably, the Gidley Quarry population was, on the whole, slightly smaller than that of Rock Bench. Such differences in local populations are not uncommon in Recent species and should be expected in extinct species as well. Furthermore, although Gidley Quarry and Rock Bench are spatially and temporally close, there may be a slight age difference. The *Elphidotarsius* specimens now known suggest that Gidley Quarry is slightly older, and plesiadapid fossils strengthen this view (P. D. Gingerich, personal communication), although Sloan (1969; fig. 5) considered Rock Bench to be the earlier of the two.

To summarize, the Rock Bench Quarry sample of *Elphidotarsius* is best referred to *E. florencae*. The possibility cannot be dismissed, however, that additional specimens from Gidley Quarry or an equivalent level nearby could reveal sufficient distinctions from the Rock Bench population to warrant specific separation for the latter.

Three specimens (PU Nos. 16916, 19764, and 19780) from the Medicine Rocks (Tongue River Formation) near Ekalaka, Montana, are also tentatively referred to

Figure 8. Above: *Elphidotarsius*, cf. *E. florencae* Gidley, PU 17439, right maxilla with P^3–M^3. Crown view. × 6. Rock Bench Quarry. Below: *Elphidotarsius shotgunensis* Gazin, holotype, AMNH 88311, right P_4–M_1. Crown view. × 6.

E. florencae. All are fragmentary mandibles with partial dentition, but only one specimen, PU 19764, preserves all of P_4. In P_4 of this specimen, the presumed homologues of the molar trigonid cusps are prominent, with both paraconid and metaconid situated slightly lingual to the protoconid. The fourth, anteriormost cusp is much lower and very small, smaller than in other specimens referred to *E. florencae.* Whether this feature is significant taxonomically is unclear at present; PU 19764 is

otherwise like the holotype and the Rock Bench specimens.

Elphidotarsius shotgunensis Gazin, 1971
Figures 4C, 8

Elphidotarsius shotgunensis Gazin, 1971: 33.

Holotype: AMNH 88311, right mandibular fragment with P_4-M_1 and anterior alveoli.

Hypodigm: Type and MCZ 18775,[1] a right M_1.

Horizon and Locality: Late Middle Paleocene (late Torrejonian), Shotgun Member, Fort Union Formation: near Cottonwood Creek, Sect. 30–31, T. 6 N., R. 3 E., Wind River Basin, Wyoming.

Diagnosis (modified after Gazin): P_4 longer and narrower than in *E. florencae;* M_1 narrower than in *E. florencae.* Primary portion of P_4 with 4 apical cusps, possibly less well defined than in *E. florencae.* Trigonid of M_1 more elongate than in *E. florencae*, i.e., paraconid and metaconid more widely separated, but both lingually placed with respect to protoconid.

Discussion: Gazin described this form thoroughly, and there is no new material since his study to contribute further information. A re-examination of the type mandible, however, results in a different interpretation of the anterior dentition. The three alveoli immediately anterior to P_4 probably held P_3, P_2, and the canine. Anterior to the canine, Gazin suggests the presence of three incisors. This is very unlikely, for no known Paleocene primate had three lower incisors. The most anterior alveolus is enlarged and anteriorly inclined, as in other carpolestids. It is followed by a smaller alveolus, for I_2. Gazin interpreted a groove behind this as possibly the alveolus of a third incisor, but the groove is small and poorly defined, and it appears to be situated at a break in the mandible. It is most improbable that it represents an alveolus. (It should be noted that Gazin was duly hesitant in suggesting the presence of three incisors.) Specimens

[1] This specimen has apparently been lost.

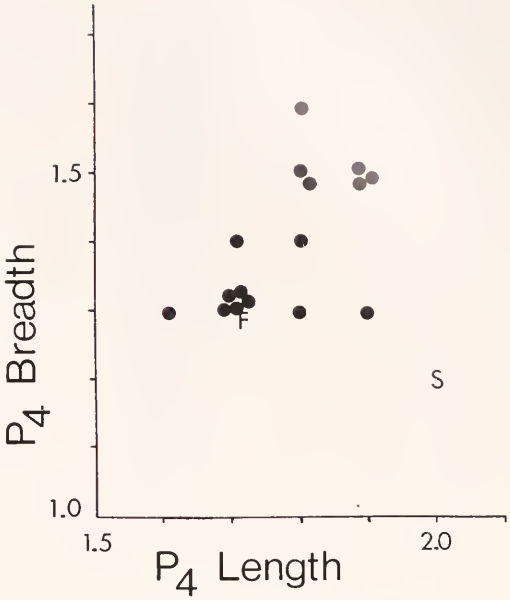


Figure 9. Scatter diagram of P_4 dimensions of *Elphidotarsius.* Black circles = *E.*, cf. *E. florencae* from Rock Bench Quarry. F = *E. florencae*, holotype, from Gidley Quarry. S = *E. shotgunensis*, holotype.

of *Elphidotarsius* from Rock Bench Quarry, discussed above, indicate the presence of only two lower incisors.

Gazin referred an upper premolar, MCZ 18774, to this species. Inspection of the specimen and comparison with other carpolestids reveals that it is a very water-worn premolar of *Carpodaptes,* also known from this locality. With the elimination of this specimen, the known teeth of *E. shotgunensis* are reduced to P_4 and M_1. Nevertheless, the morphology of these two is clearly more advanced than in *E. florencae* and suggests a trend toward *Carpodaptes.*

Carpodaptes Matthew and Granger, 1921

Carpodaptes Matthew and Granger, 1921: 6; Simpson, 1935: 10; Dorr, 1952: 82.

Type Species: *Carpodaptes aulacodon* Matthew and Granger, 1921.

Included Species: *C. aulacodon, C. hazelae, C. hobackensis, C. cygneus,* and *C. jepseni* (new species).

Distribution: Late Middle Paleocene (late Torrejonian) of Wyoming, Late Paleocene (Tiffanian) of western North America: Alberta, Saskatchewan, Montana, North Dakota, Wyoming, and Colorado.

Emended Diagnosis: Lower dental formula 2.1.2.3. Enlarged medial incisor longer and more slender than in *Elphidotarsius*. Lateral incisor (I_2?), C, and P_3 reduced to tiny, single-rooted vestiges with buttonlike crowns. P_2 absent. P_4 larger, both relatively and absolutely, than in *Elphidotarsius*, but smaller in both respects than in *Carpolestes;* apical cusps numbering 5 or 6, followed by talonid heel less distinct than in *Elphidotarsius*, but generally more distinct than in *Carpolestes;* heel decidedly lower than trigonid of M_1; slight constriction of enamel at crown separating talonid from primary blade. Trigonid of M_1 elongate and open, paraconid immediately anterior or slightly anterolingual to protoconid; protoconid the most prominent trigonid cusp. M_{2-3} not significantly different from those of *Elphidotarsius* and *Carpolestes*, but third lobe of M_3 usually larger than in *Elphidotarsius;* incipient mesoconid sometimes present on cristid obliqua of M_3. Upper dentition with at least two reduced teeth anterior to P^3 (presumably P^2 and C); both with one major cusp. P^{3-4} pyriform, polycuspate, greatly enlarged over those of *Elphidotarsius*, but not so large as in *Carpolestes*. P^3 and P^4 subequal, or P^3 slightly smaller than P^4, both larger than molars; each with 3 well-developed longitudinal rows of cuspules, buccal row longest. P^3 without pronounced anteroexternal spur typical of *Carpolestes;* external row with 4 cusps, the most anterior separated somewhat from the 3 posterior; median row a crescentic crest, with one or more cuspules, situated slightly buccal to middle of tooth; lingual section with two subequal cusps. P^4 with buccal row of 5 or 6 cusps, the 2 anterior ones separated slightly from the 3 or 4 posterior ones; median crest similar to that of P^3; lingual region with 3 cusps, the central cusp largest. Molars very similar morphologically to those of other carpolestid genera.

Carpodaptes aulacodon Matthew and Granger, 1921

Figures 10, 11A

Carpodaptes aulacodon Matthew and Granger, 1921: 6; Simpson, 1935b: 12.

Holotype: AMNH 17367, left mandible with P_3-M_3.

Hypodigm: Type specimen only.

Horizon and Locality: Late Paleocene (Tiffanian), Tiffany Formation: Mason Pocket, Tiffany, Colorado.

Emended Diagnosis: P_4 bearing 5 poorly-defined apical cusps, followed by distinctly separated, low talonid heel; anteriormost cusp almost indistinct, as low as talonid and separated somewhat from following 4 closely appressed cusps; lateral profile roughly triangular with apex almost pointed, in contrast to more gently rounded profiles of P_4 in other species of *Carpodaptes*. P_4 longer than in *C. hazelae, C. hobackensis*, or *C. cygneus*, shorter than in *C. jepseni* or species of *Carpolestes*. Molars not significantly different from those of other species.

Discussion: This revised diagnosis of *Carpodaptes aulacodon* is the first published since other species were added to the genus. The type mandible clearly reveals the great reduction of the teeth between the enlarged incisor and P_4, a characteristic of carpolestids which is manifested to a greater degree in *Carpolestes* and *Carpodaptes* than in *Elphidotarsius*.

The structure of P_4, the most diagnostic mandibular tooth in carpolestids, differs from that of all other species of *Carpodaptes*, and we may be confident (despite the existence of only one specimen) in recognizing AMNH 17367 as a representative of a distinct species.

Figure 10. Above: *Carpodaptes aulacodon* Matthew and Granger, holotype, AMNH 17367, left P_3–M_3. Crown view. × 6. Below: *Carpodaptes* sp., PU 14639. Left maxilla with P^4–M^2, crown view. × 6.

Carpodaptes hazelae Simpson, 1936
Figures 11C, D, 12–18

Carpodaptes hazelae Simpson, 1936: 21; Simpson, 1937a: 5.

Holotype: AMNH 33854, right mandible with P_4-M_3.

Hypodigm: Type and AMNH Nos. 33853, 33855, 33887, 33979–33985, from Scarritt Quarry; PU Nos. 19558, 19572, 19574, 19596, 19601, 19936, 19939, 19953–19955, 19958, 19968, 19969, 19985, 20007, 20010, 20011, 20034, 20060, 20064, 20065, 20068, 20084, 20087, 20610, 20615, 20630, 20634, 20656, 20719, 20808, 20812, 20820, 20839, 20840,

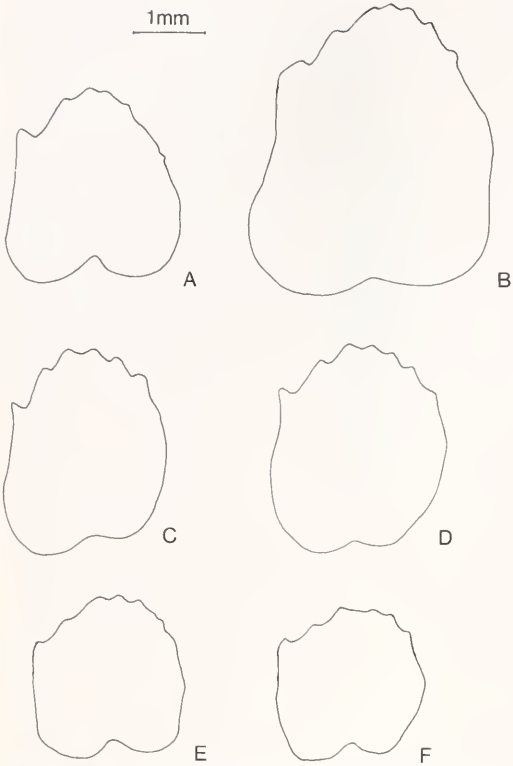


Figure 11. Outlines of right P_4 of *Carpodaptes* (lateral aspect), to same scale. A) *C. aulacodon*, holotype, AMNH 17367 (reversed). B) *C. jepseni*, holotype, PU 20716. C) *C. hazelae*, holotype, AMNH 33854 (Scarritt Quarry). D) *C. hazelae*, PU 20084 (Cedar Point Quarry). E) *C. hobackensis*, UMMP V55124. F) *C. cygneus*, holotype, ROM 05622.

20886, 20889, 20898, 20900, 21213, 21266, 21279, 21297, 21299, 21316, 21317, 21330, 21341, 21350, 21351, 21357, 21384, 21393, 21399, 21413, 21419, 21437, 21438, from Cedar Point Quarry.

Horizon and Locality: Late Paleocene (Tiffanian) of Montana and Wyoming: Scarritt Quarry, Melville Member, Fort Union Formation, Crazy Mountain Field, Montana; Cedar Point Quarry, Polecat Bench Formation, Big Horn County, Wyoming.

Emended Diagnosis: Close to *C. aulacodon* in size, but mean length of P_4 less than in *C. aulacodon*. P_4 with 5 or 6 variably defined apical cusps followed by a low but distinct talonid heel; more rounded in profile and more quadrate in occlusal view (at base) than in *C. aulacodon*. Molars not significantly different morphologically from other species, but larger than in *C. hobackensis* and *C. cygneus*, smaller than in *C. jepseni*.

Discussion: *Carpodaptes hazelae* was originally described and defined from a small sample collected at the Scarritt Quarry in the Crazy Mountain Field. The much larger sample from Cedar Point Quarry is here referred to *Carpodaptes hazelae* and necessitates the revised diagnosis presented above. *C. hazelae* is now represented by more specimens than any other species of the family.

There can be little doubt that the carpolestids from Cedar Point Quarry all represent the same species. Although considerable variation is observed, graphs of tooth dimensions reveal normal, unimodal distribution; there is no indication of sexual dimorphism and no evidence of the presence of more than one taxon. Since the different variations do not fall into consistently distinct groups, there is no practicable method of distinguishing more than one species, and indeed, no justification for so doing. On the other hand, a casual examination of some of the specimens here referred to *C. hazelae* might suggest that the Cedar Point Quarry sample represents a species distinct from that of Scarritt Quarry. But, as noted above, separate populations of a species not uncommonly show minor differences, and this should not be unexpected in *C. hazelae*. The large sample of this species now known provides us with a good cross-section of the variation which may occur intraspecifically in carpolestids, and it is substantial. But almost all variation is limited to the specialized premolars, P_4 and P^{3-4}. Although some specimens in the Cedar Point sample differ in size or in minor morphologic details from the type specimen (from Scarritt Quarry), others are virtually identical to the type. The Scarritt Quarry specimens tend to be slightly larger and their lower cheek teeth (P_4-M_3) relatively broader than the mean

Figure 12. *Carpodaptes hazelae* Simpson, AMNH 33980, left dentary with P_4–M_3. Crown view (above) and lateral view (below). × 6. Scarritt Quarry.

values for the Cedar Point sample, but several Cedar Point specimens exceed in size even the largest Scarritt specimen. P_4 in the best preserved individuals from Scarritt Quarry bears 5 sharp, relatively large apical cuspules followed by a lower, distinct talonid heel (Fig. 12). In the Cedar Point specimens, the apical cuspules, 5 or 6 in number, are usually (but not always) less well defined (Fig. 16). The sixth cuspule arises low at the anterior of the blade in about 75% of the known specimens (44 of

Figure 13. Above: *Carpodaptes hazelae* Simpson, AMNH 33980, left maxilla with P^2–M^3. Crown view. × 6. Scarritt Quarry. Below: *Carpodaptes hazelae* Simpson, PU 19939, right maxilla with P^3–M^3, crown view. × 6. Cedar Point Quarry.

Figure 14. *Carpodaptes hazelae* Simpson, PU 20839, right dentary with P_4–M_3. Crown view (above) and lateral view (below). × 6. Cedar Point Quarry.

59 specimens); it is variably developed, ranging from an incipient cuspule to one as well defined as any of the other apical cusps. The talonid of P_4 in the Cedar Point specimens is usually not so distinctly set off from the blade as in the Scarritt individuals, but this feature, too, is variable.

Only a few upper dentitions are known for *Carpodaptes hazelae*. The Scarritt Quarry and Cedar Point Quarry specimens are similar except for the position of one cusp on P^4 (Fig. 18). In the lingual section of P^4 in three Scarritt specimens, the central cusp (the largest of the three lingual cusps) is situated approximately between the other two lingual cusps and contributes to the lingual face of the tooth. This same cusp in the two known specimens from Cedar Point is situated posterolabial to the anteriormost lingual cusp, thus it contributes almost nothing to the lingual face of the tooth. The fourth Scarritt specimen

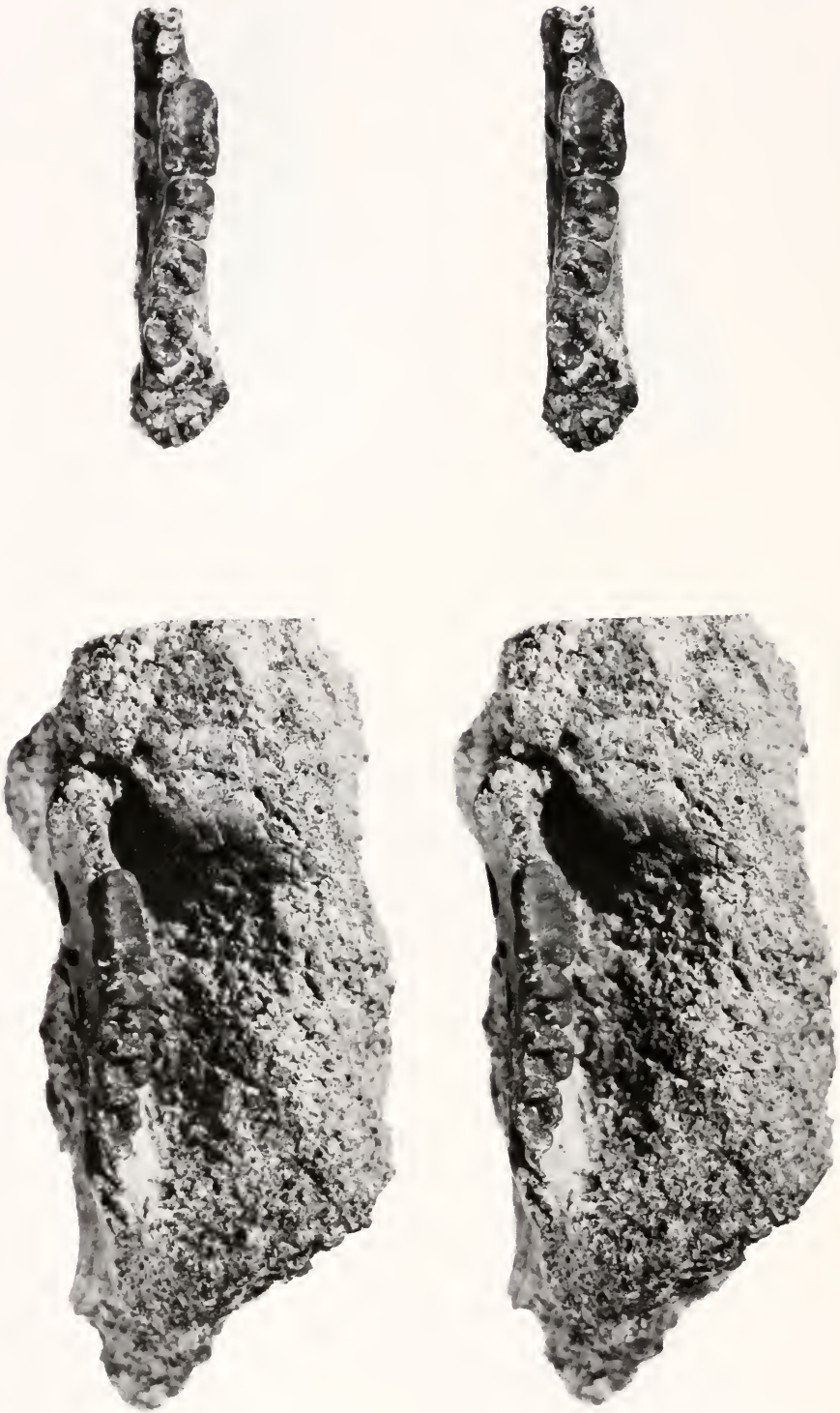


Figure 15. *Carpodaptes hazelae* Simpson. Above: PU 21350, right dentary with P_4–M_3, crown view. Below: PU 21351, right dentary with P_4–M_3, crown view. × 6. Cedar Point Quarry.

Figure 16. *Carpodaptes hazelae* Simpson. Above: PU 21351, right dentary with P_4–M_3, medial view. Note presence of 6 apical cusps. Below: PU 21350, right dentary with P_4–M_3, medial view. Note presence of 5 apical cusps. Both × 6. Both from Cedar Point Quarry.

preserving P_4 (AMNH 33981) is nearly intermediate between these two morphologies, suggesting that the difference is not taxonomically significant.

In addition to the Scarritt Quarry and Cedar Point Quarry remains referred to this species, there are a few specimens from the Late Torrejonian Shotgun Local Fauna (MCZ Nos. 18763, 18776, 18777, 19683, 19684) that are closely comparable to *C. hazelae*. They are the earliest recorded representatives of the genus *Carpodaptes*, and the only ones known from pre-Tiffanian sediments.

An isolated P_4 (UMVP 5007) from the Circle Local Fauna, Tongue River Formation, near Circle, Montana, is probably referable to *C. hazelae*.

Specimens of *Carpodaptes* from the Ravenscrag Formation in Alberta were referred to *Carpodaptes*, cf. *C. hazelae*, by Krishtalka (1973), although (as he noted) they are smaller than typical *C. hazelae*. They are closer in size and morphology to *Carpodaptes cygneus* and are here tentatively referred to the latter.

The dental morphology of *C. hazelae* has been described in detail by Simpson (1936, 1937a). No new material has been recovered from Scarritt Quarry since Simpson's work, and the material he described in 1937 still includes some of the most complete carpolestid specimens known. Among the Cedar Point specimens are several which preserve the anterior portion of the mandible, but only alveoli are preserved anterior to P_3. From these specimens it is clear that there were three diminutive, single-rooted teeth between the large medial incisor and P_4. I interpret these as a lateral incisor, the canine, and P_3. P_3 is preserved in only one specimen, PU

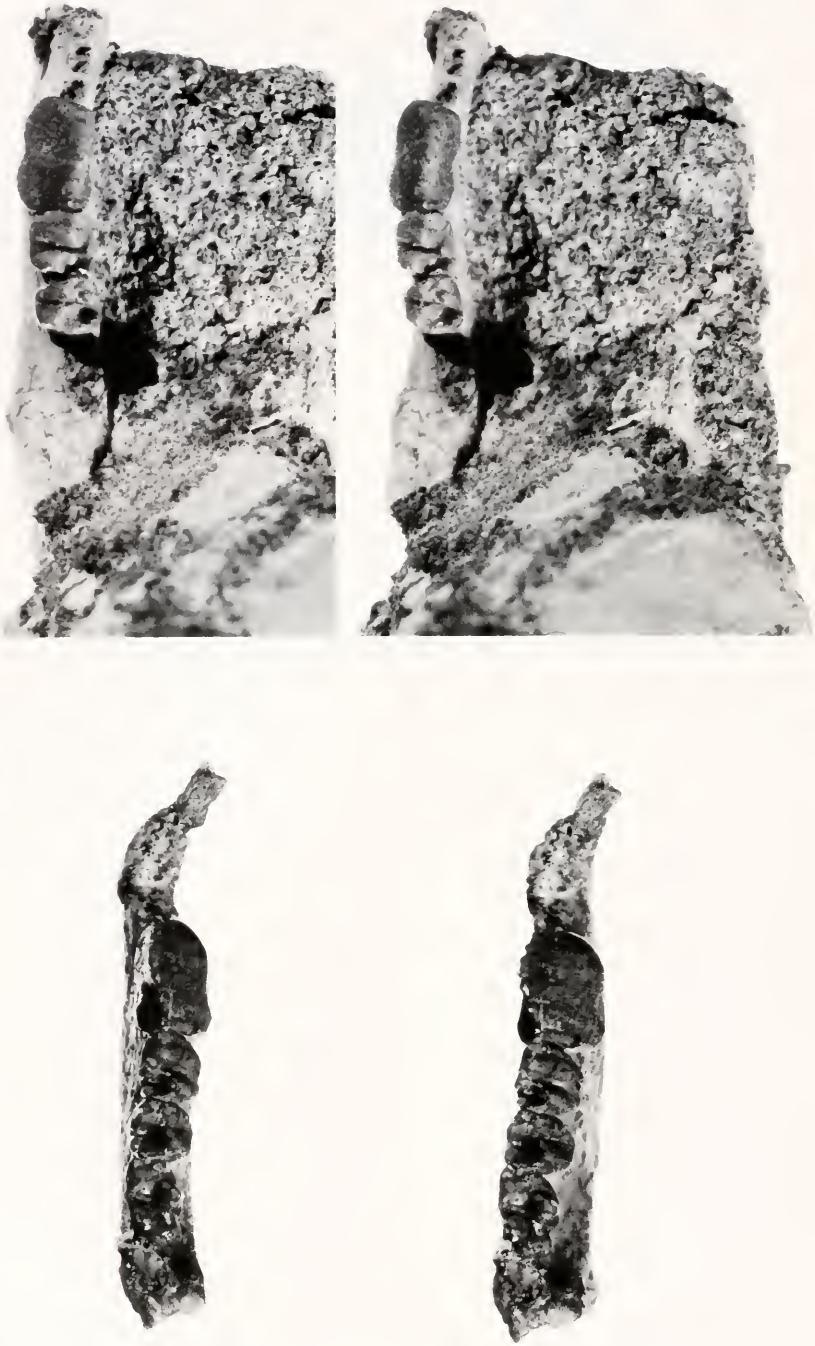


Figure 17. *Carpodaptes hazelae* Simpson. Above: PU 21297, left dentary with P_4–M_2, crown view. Below: PU 20084, right dentary with P_4–M_3, crown view. Both × 6. Both from Cedar Point Quarry.

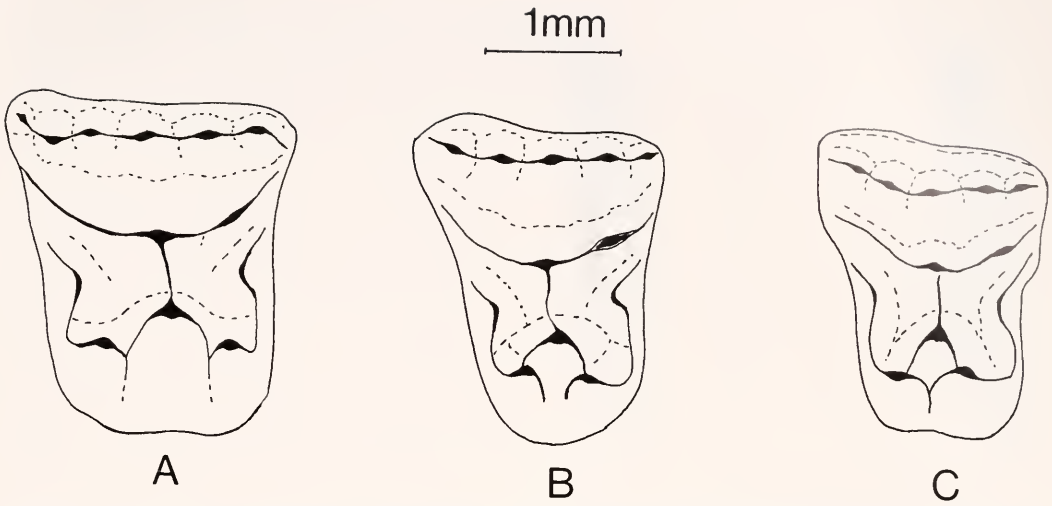


Figure 18. Crown view of right P^4 of *Carpodaptes hazelae*, to same scale. A) AMNH 33980 (reversed), from Scarritt Quarry. B) AMNH 33981, from Scarritt Quarry. C) PU 19939, from Cedar Point Quarry.

20630, and is much reduced compared to that of *Elphidotarsius*. It is a vestigial peg-like tooth, with the same morphology as P_3 in *C. aulacodon* (and similar, in fact, to P_3 in *Carpolestes*). The morphology of P_4 has been discussed above. It should be emphasized again that although P_4 is unquestionably the most diagnostic mandibular tooth in carpolestids, it is also the most variable. The extent of its variability is especially well demonstrated in the large sample of *C. hazelae*.

The molars (lower and upper) of the Cedar Point specimens are virtually indistinguishable from those of the Scarritt Quarry specimens. There is some variation, of course, in relative proportions (e.g., relative breadth of the lower molars).

A maxillary dentition (AMNH 33980) from Scarritt Quarry, described by Simpson (1937a), included two small, single-rooted teeth anterior to P^3. Unfortunately, the anteriormost of these (C?), unknown in any other carpolestid specimen, has been

TABLE 2. METRICAL DATA FOR LOWER CHEEK TEETH OF *CARPODAPTES HAZELAE*, COMBINED SAMPLES FROM SCARRITT AND CEDAR POINT QUARRIES.

		N	OR (mm)	$\bar{x}$	s	V
P_4	length	56	2.1–2.8	2.46 ± .02	.142 ± .013	5.8 ± .5
	breadth	55	1.2–1.8	1.54 ± .02	.134 ± .013	8.7 ± .8
M_1	length	53	1.3–1.6	1.47 ± .01	.078 ± .008	5.3 ± .5
	breadth	52	1.2–1.6	1.34 ± .01	.097 ± .010	7.2 ± .7
M_2	length	39	1.1–1.4	1.29 ± .01	.070 ± .008	5.4 ± .6
	breadth	39	1.2–1.6	1.36 ± .01	.091 ± .010	6.7 ± .8
M_3	length	17	1.7–2.0	1.86 ± .02	.093 ± .016	5.0 ± .9
	breadth	17	1.0–1.4	1.18 ± .02	.103 ± .018	8.7 ± 1.5
Mandibular depth		36	3.1–4.0	3.49 ± .04	.228 ± .027	6.5 ± .8

TABLE 3. METRICAL DATA FOR LOWER CHEEK TEETH OF *CARPODAPTES HAZELAE* FROM CEDAR POINT QUARRY ONLY.

		N	OR (mm)	$\bar{x}$	s	V
P_4	length	53	2.1–2.8	2.46 ± .02	.143 ± .014	5.8 ± .6
	breadth	52	1.2–1.8	1.53 ± .02	.132 ± .013	8.6 ± .8
M_1	length	47	1.3–1.6	1.46 ± .01	.077 ± .008	5.3 ± .5
	breadth	46	1.2–1.5	1.32 ± .01	.087 ± .009	6.6 ± .7
M_2	length	33	1.1–1.4	1.29 ± .01	.070 ± .009	5.4 ± .7
	breadth	33	1.2–1.5	1.34 ± .01	.079 ± .010	5.9 ± .7
M_3	length	14	1.7–2.0	1.86 ± .03	.101 ± .019	5.4 ± 1.0
	breadth	14	1.0–1.3	1.16 ± .03	.094 ± .018	8.1 ± 1.5
Mandibular depth		33	3.1–4.0	3.46 ± .04	.221 ± .027	6.4 ± .8

lost since Simpson's description. Both P^3 and P^4 are hypertrophied and specialized in *C. hazelae*. P^4 has 5 or 6 buccal cuspules, the two anterior ones closely associated and separated slightly from the three or four posterior cuspules. The specialization of P^3 is especially dramatic in comparison to the small, generalized P^3 of *Elphidotarsius*. Morphological details of P^3 and P^4 in *C.* hazelae have been listed above in the diagnosis of *Carpodaptes* and in Simpson's (1937a) description.

Carpodaptes hobackensis Dorr, 1952
Figures 11E, 19, 20A

Carpodaptes hobackensis Dorr, 1952: 82.

Holotype: UMMP 27233, left mandible with I_1, P_4-M_3, and roots of I_2, C, P_3.

Hypodigm: Type and UMMP Nos. 27234, 27253, 55124.

Horizon and Locality: Late Paleocene (Tiffanian), Dell Creek Local Fauna, Hoback Formation: UM-Sub-Wy Locality No. 1, Dell Creek Quarry, Sublette County, Wyoming.

Diagnosis (modified after Dorr, 1952): About the same size as *C. cygneus* but smaller than all other known species of *Carpodaptes*. P_4 lower and more gently rounded in lateral profile than in other species of *Carpodaptes*, except *C. cygneus;* crest S-shaped in occlusal view due to deep posterointernal excavation of tooth, bearing 5 small but distinct apical cusps and a talonid cusp; talonid not so clearly separated from main blade as in *C. hazelae* or *C. aulacodon;* incipient lower anterior

TABLE 4. METRICAL DATA FOR LOWER CHEEK TEETH OF *CARPODAPTES HAZELAE* FROM SCARRITT QUARRY ONLY.

		N	OR (mm)	$\bar{x}$	s	V
P_4	length	4	2.5–2.6	2.58 ± .03	.050 ± .018	1.9 ± .7
	breadth	4	1.7	1.70	0	0
M_1	length	7	1.4–1.6	1.51 ± .03	.069 ± .018	4.6 ± 1.2
	breadth	7	1.4–1.6	1.47 ± .03	.076 ± .020	5.1 ± 1.4
M_2	length	7	1.2–1.5	1.34 ± .04	.098 ± .026	7.3 ± 2.0
	breadth	7	1.4–1.6	1.47 ± .03	.076 ± .020	5.1 ± 1.4
M_3	length	4	1.8–2.0	1.90 ± .04	.082 ± .029	4.3 ± 1.5
	breadth	4	1.2–1.4	1.28 ± .05	.096 ± .034	7.5 ± 2.7
Mandibular depth		4	3.7–3.8	3.75 ± .03	.058 ± .021	1.5 ± .5

seventh cusp variable in occurrence; tooth very similar to that of *C. cygneus,* differing in having less pronounced vertical ribs developed beneath apical cusps on lingual side, less developed posterior apical cusp (cusp just anterior to talonid heel), and, consequently, a deeper posterolingual depression than in *C. cygneus;* weakly expressed posterointernal cingulum present, extending forward beyond midpoint of tooth. Weak internal cingulum at base of trigonid of M_1.

Discussion: This species is very close to the subsequently described species *C. cygneus* (L. S. Russell). Specimens now known reveal minor but apparently consistent differences between the two, and both are accordingly retained as valid taxa in this review. They are so similar, however, that they must be very closely related, and it is not inconceivable that future evidence could provide justification for placing *C. cygneus* in synonymy.

Although only four specimens are known (no upper teeth have been recovered) the entire lower dentition is represented. The type mandible preserves parts or all of the lower teeth. The enlarged incisor unfortunately was damaged in preparation, but as restored it is a relatively longer and more slender tooth than in *Elphidotarsius,* much closer to the enlarged incisor of *Carpolestes.* This is the only incisor of *Carpodaptes* known, except for one isolated tooth from the Shotgun Local Fauna (UW 6530), possibly from *Carpodaptes* sp. (see Fig. 5B). Though only roots of the I_2, C, and P_3 remain, their crown shapes are clearly indicated by impressions in the matrix. All were diminutive, single-rooted, peglike teeth with bulbous crowns.

P_4, with its posterointernal depression, S-shaped crest, and talonid less distinctly separated from the main blade than in other species of *Carpodaptes,* bears a closer resemblance to P_4 of *Carpolestes* than does P_4 of any other species of *Carpodaptes,* except possibly *C. jepseni* (which in other ways foreshadows *Carpolestes*). For these reasons Dorr (1952: 84) suggested indirectly that *C. hobackensis* might be closer to the ancestry of *Carpolestes* than any other species of *Carpodaptes* then known. The diminutive size of *C. hobackensis* relative to other species of *Carpodaptes* casts doubt on such a possible relationship, however.

Figure 19. *Carpodaptes hobackensis* Dorr, UMMP V55124, right dentary with P_4–M_3. Crown view (above) and medial view (below). × 6.

No additional specimens have been recovered since Dorr's report. His thorough description obviates the need for further detail here.

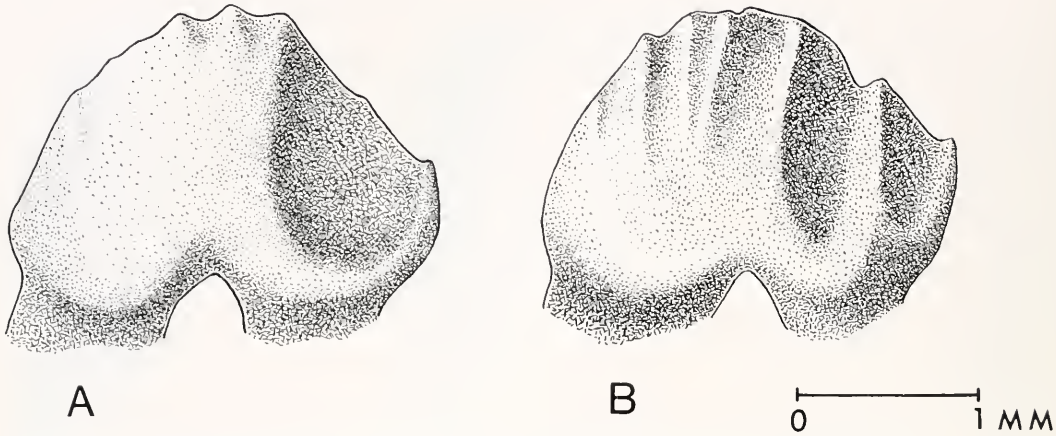


Figure 20. Lingual view of right P_4 of A) *Carpodaptes hobackensis*, and B) *Carpodaptes cygneus*.

Carpodaptes cygneus (L. S. Russell), 1967
Figures 11F, 20B

Carpolestes cygneus L. S. Russell, 1967: 19.

Holotype: ROM 05622, right mandibular fragment with P_4.

Hypodigm: Type and paratypes, ROM Nos. 05623 and 05624, from Swan Hills, Alberta; numerous specimens in the University of Alberta collection from near Roche Percee, Saskatchewan, including UA Nos. 8733, 8742, 8799, 8800.

Horizon and Locality: Late Paleocene (early [?] Tiffanian) of Alberta and Saskatchewan: Paskapoo Formation of the Swan Hills, north-central Alberta, and Ravenscrag Formation of southern Saskatchewan (and Alberta?).

Emended Diagnosis: Small carpolestids near *Carpodaptes hobackensis* in size but smaller than other known species. P_4 with 5 or 6 small apical cusps; posterior cusp (anterior to talonid cusp) well expressed; vertical ribs beneath apical cusps on lingual side pronounced, noticeably better developed than in *C. hobackensis;* postero-internal depression not as deep as in *C. hobackensis.*

Discussion: Russell named this species on the basis of three jaw fragments each holding a single tooth: two lower fourth premolars and one upper third premolar. Fortunately, these are the most diagnostic teeth. Russell regarded the species as closest to *Carpolestes dubius* and cited the resemblances between the two as justification for allocating the new species to the genus *Carpolestes.* As Krishtalka (1973) pointed out, all the features noted by Russell are characteristic of *Carpodaptes;* there is no special resemblance to *Carpolestes.* In fact, *C. cygneus* is remarkably close to *C. hobackensis,* a form described fifteen years earlier. The only noticeable differences in the dentition as known occur in P_4; these have been detailed above under *C. hobackensis* (See also Fig. 20).

A large sample recently recovered from the Ravenscrag Formation of Saskatchewan by D. Krause (personal communication) is referable to *C. cygneus.* Many specimens are considerably more complete than Russell's original lot and show the mandibular dentition, other than P_4, to be virtually indistinguishable from that of *C. hobackensis.* A thorough description of these will be published by Krause.

P^3, known from one of the paratypes (ROM 05624) and a few of Krause's specimens, shows some distinctions from that of *C. hazelae* (the only other species of the genus in which upper teeth are known). ROM 05624 is smaller and more square in

occlusal view than P^3 of *C. hazelae.* In the posterior third of the tooth there is a short invagination of the posterior wall in the form of a crest roughly parallel to, and between, the median and lingual cusp rows. This crest is present also in UA 8799, from the Ravenscrag of Saskatchewan (but this tooth is closer in shape to that of *C. hazelae* than to ROM 05624).

Krishtalka (1973) referred a sample from the Ravenscrag of Alberta to *Carpodaptes,* cf. *C. hazelae.* In size and P_4 morphology, the specimens are more like *C. cygneus* than *C. hazelae,* and are here designated *Carpodaptes* sp., cf. *C. cygneus.* One of these is a P^3 (UA 5857) which lacks the crest observed in ROM 05624 and UA 8799.

Also allocated tentatively to *C. cygneus* are a few isolated teeth (UMVP collection, uncatalogued) from Tiffanian deposits of the upper Tongue River Formation at Olive, Montana.

R. C. Holtzman (personal communication) has recently collected specimens of *Carpodaptes* from the lower part of the Tongue River Formation near Judson, North Dakota (UMVP Nos. 6062, 6063, 6142, 6190, 6217, 6355, 6517, and 6518). They show resemblances to both *C. cygneus* and *C. hobackensis.* UMVP Nos. 6062 and 6142 lack the prominent lingual ridge beneath the last apical cusp of P_4, a characteristic of *C. cygneus,* consequently showing the posterolingual hollowing typical of *C. hobackensis.* On the other hand, UMVP Nos. 6063 and 6190, in which the ridge is well developed in P_4, are like *C. cygneus.* The Judson sample may represent the sympatric occurrence of the two species, but suggests that they may be synonymous. Description of the specimens is in preparation by Holtzman.

Carpodaptes jepseni, new species
Figures 11B, 21

Etymology: Named for the late Professor Glenn Lowell Jepsen, in recognition of his outstanding contributions to our knowledge of Paleocene mammals, and in particular for his efforts in the recovery of the majority of known carpolestid specimens.

Holotype: PU 20716, right mandible with P_4-M_2.

Hypodigm: Type specimen only.

Horizon and Locality: Late Paleocene (Tiffanian), Polecat Bench Formation: Divide Quarry, NE 1/4, SW 1/4, Sect. 16, T. 54 N., R. 95 W., Big Horn County, Wyoming.

Diagnosis: Largest known species of *Carpodaptes,* about the size of *Carpolestes nigridens* and *dubius.* P_4 very high crowned, bearing 6 well-developed apical cusps followed by lower, separate talonid heel; last apical cusp lower but better developed than those anterior to it, as in *C. cygneus;* talonid lower than trigonid of M_1, and distinctly separated from main blade as in *C. hazelae* and *C. aulacodon;* lateral profile close to that of *C. aulacodon,* approaching a more pointed form than in other species. Paraconid of M_1 only slightly subordinate to protoconid. Molars longer and broader than in other species.

Discussion: This problematical specimen shows features which resemble both *Carpodaptes* and *Carpolestes,* but it does not fit very conveniently into either. The balance of features, however, seems to weigh in favor of *Carpodaptes,* to which it is here referred. At present, this is preferable to a proposal of a new genus.

The number and clarity of the apical cusps of P_4 are characteristic of *Carpodaptes,* as are the well-developed sixth apical cusp and the distinctly lower and well separated talonid cusp. These features are not found in *Carpolestes.* On the other hand, the large size, high crown, and the relative size of P_4 to the molars are much more like *Carpolestes.* The species could therefore be regarded either as a less specialized representative of *Carpolestes* or as a large, relatively advanced representative of *Carpodaptes.*

The age of Divide Quarry is not yet well established, but it appears to be later than

Figure 21. *Carpodaptes jepseni*, new species, holotype, PU 20716, right dentary with P_4–M_2. Crown view (above) and medial view (below). × 6.

Cedar Point Quarry, which yields *Carpodaptes hazelae*, and earlier than Princeton Quarry, which yields *Carpolestes dubius* (D. C. Parris, *in litt.*, 2/18/72). It appears, then, that *C. jepseni* is both structurally and stratigraphically intermediate between *Carpodaptes* and *Carpolestes*. It is probably in or very near the ancestry of *Carpolestes*.

The posterior portion of a P_4 (PU 20852) from Long Draw Quarry, Carbon County, Montana, is possibly referable to *C. jepseni*.

Carpodaptes sp.
Figure 10

A maxillary fragment (PU 14639) from Princeton Locality 11 in the Crazy Mountain Field, Montana, preserves left P^4-M^2. It is close in size to *Carpodaptes hazelae*, but P^4 is more triangular (lingually compressed) and relatively more extended buccolingually than in *C. hazelae*. In the orientation of the three lingual cusps of P_4, PU 14639 resembles the Cedar Point speci-

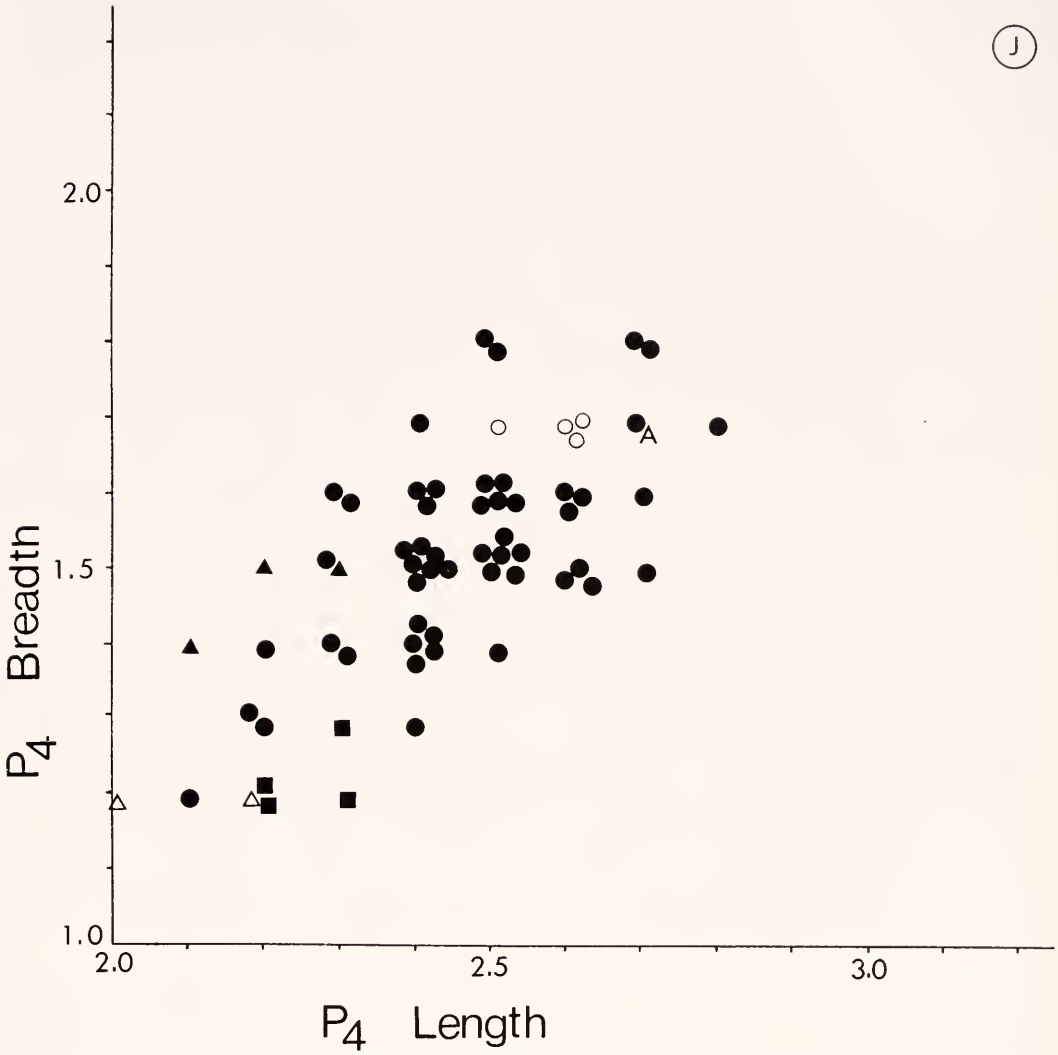


Figure 22. Scatter diagram of P_4 dimensions of *Carpodaptes*. Black circles = *C. hazelae* from Cedar Point Quarry. Open circles = *C. hazelae* from Scarritt Quarry. Black squares = *C. hobackensis*. Open triangles = *C. cygneus* from Swan Hills. Black triangles = *C.*, cf. *C. cygneus* from Cypress Hills, Alberta. A = *C. aulacodon*, holotype. Circled J = *C. jepseni*, holotype.

mens more closely than those of Scarritt Quarry. Locality 11 (Simpson, 1937b: 41) is approximately 1000 feet stratigraphically above the Scarritt Quarry, thus it is possible that this specimen represents a hitherto undescribed species. Bell (1941), in an unpublished thesis, based a new species on PU 14639. In view of the small number of maxillary dentitions known for this genus, and the high degree of intraspecific variability present in large samples (of lower teeth, for example) it seems more appropriate for the present to refer this to *Carpodaptes* sp. than to propose a new taxon.

Carpolestes Simpson, 1928

Carpolestes Simpson, 1928: 7.
Litotherium Simpson, 1929: 9.

Type Species: *Carpolestes nigridens* Simpson, 1928

Type Species of Synonym: *Litotherium complicatum* Simpson, 1929.

Included Species: *C. nigridens* and *C. dubius*.

Distribution: Latest Paleocene ("Clarkforkian") and earliest Eocene (Wasatchian) of Montana and Wyoming.

Emended Diagnosis: Largest, most specialized carpolestids. Dental formula $\frac{?2.?1.?3.3}{2.\ 1.\ 2.3}$. Anterior lower dentition much as in *Carpodaptes*. Enlarged medial incisor anteriorly inclined, long, slender. Alveolus of I_2 indicating very reduced, peglike tooth. Canine and P_3 tiny, single-rooted, crowns buttonlike; crown of C with slight anterior overhanging projection. P_4 bladelike, very high crowned, relatively very large (almost twice as long as M_1); apex considerably higher than any other tooth; enamel of buccal side extending downward much below enamel of any other tooth, and relatively lower than in *Carpodaptes*. 8 to 9 apical cuspules closely spaced, varying in expression from tiny and sharp to nearly indistinguishable traces; talonid merging with main blade, height equaling that of trigonid of M_1; latter forming continuation of P_4 blade. Trigonid of M_1 with paraconid situated directly anterior to protoconid, both cusps equally prominent. M_{2-3} slightly larger than in other two genera, sometimes with incipient mesoconid.

At least 3 teeth present anterior to P^2. P^2 reduced, single-rooted, with one main cusp, as in *Carpodaptes*. P^{3-4} polycuspate, greatly enlarged, noticeably larger than molars; cuspule development as in *Carpodaptes*, but teeth larger, relatively longer; P^3 larger than P^4, with variable anteroexternal extension ("spur"). Upper molars larger but otherwise similar to those of *Carpodaptes*. Mandible deeper than in other two genera.

Discussion: *Carpolestes* is well represented by more than 80 specimens, many of them unusually complete. All of the lower teeth except I_2 are known, and many more upper dentitions of this genus are preserved than of the other two combined. One specimen (PU 17978) includes the root or alveolus of each of three teeth anterior to P^2, presumed to have been two incisors and a canine (see p. 37).

Two nearly complete palates (PU Nos. 17709, 19422) of *Carpolestes dubius* reveal the presence of palatal vacuities. They may have been characteristic of all carpolestids, but no palatal evidence is available for the other two genera. There are no palatal vacuities in *Plesiadapis*.

Szalay (1972b) proposed that *Carpolestes* be regarded as a junior synonym of *Carpodaptes* on the premise that the number of apical cusps of P_4 might not be a valid generic criterion. From the descriptions and discussions presented above, it is clear that this criterion (and others) are real distinctions separating the late Paleocene carpolestids into two groups which deserve generic rank. As noted above, *Carpolestes* is more specialized in several features than *Carpodaptes*.

Carpolestes nigridens Simpson, 1928
Figures 23, 27A, 27B

Carpolestes nigridens Simpson, 1928: 7.
Litotherium complicatum Simpson, 1929: 10.
Carpolestes aquilae Simpson, 1929: 10.

Holotype: AMNH 22159, right mandible with P_1-M_3.

Holotype of *L. complicatum*: AMNH 22196, left P^3.

Holotype of *C. aquilae*: AMNH 22233, right mandible with P_4-M_3.

Hypodigm: Types and AMNH Nos. 22187–22190, CM Nos. 11518, 11524, 11549, 11557, 11665, 11702, and PU No. 20718, from Bear Creek; PU Nos. 17978, 19543, from "Clark Fork" beds, Bighorn Basin; and YPM Nos. 24614 and 24615, from Paint Creek.

Horizon and Locality: latest Paleocene ("Clarkforkian") of Montana and Wyoming and earliest Eocene (Wasatchian) of Wyoming: Eagle Coal Mine, Beer Creek, Montana (Fort Union Formation); Paint Creek Locality and other sites in the Bighorn Basin, northwestern Wyoming (Polecat Bench Formation).

Emended Diagnosis: P^3 differing from that of *C. dubius* in having 5 prominent buccal cusps, with anterior one fully as developed as others, resulting in noticeably more elongate anteroexternal "spur" (projection); anterior 2 cusps slightly separated from posterior 3.

Discussion: Simpson (1929: 10) diagnosed *C. aquilae* as follows: "Length P_4-M_2, 6.2 mm. P_4 about 10% smaller than in *C. nigridens* and slightly smaller relative to the molars. Molars relatively narrower basally." It is now almost certain that the features cited by Simpson are typical of individual (intraspecific) variation, and that there are no characters (within the known, limited fossil evidence) that consistently separate these two species. They are therefore synonymized.

Only one P^3 (AMNH 22196) has been recovered from Bear Creek, the locality of the type mandible, but it is undoubtedly from the same species. Examination of all known specimens of *Carpolestes* reveals no consistent differences in size or morphology between *C. nigridens* and *C. dubius* except in the form of P^3 (Figs. 27, 28). AMNH 22196 has five distinct buccal cusps, the anterior two forming a pronounced anterolateral projection. Consequently, the length of the buccal side of the tooth is nearly twice that of the lingual side. Three other specimens (PU 17978, 19543, YPM 24614) reveal a P^3 of similar form and are here referred to *C. nigridens*. Although some variation in the morphology of P^3 does occur in *C. dubius*, no individual shows such a pronounced anteroexternal spur as in *C. nigridens*.

It may be significant that all the specimens here allocated to *C. nigridens* come from sites generally regarded as later "Clarkforkian" or Wasatchian in age, while those that can be definitely referred to *C. dubius* are from the earliest "Clarkforkian" Princeton Quarry level (Silver Coulee beds). Since the one diagnostic feature of *C. nigridens* is a further specialization of P^3 over that of *C. dubius*, it would be expected to occur stratigraphically higher.

PU 17978 contains, in addition to P^3, the root of P^2, an alveolus for the canine (?), and roots of two more anterior teeth, interpreted as incisors. Unfortunately the maxillary-premaxillary suture is indiscernible, due to poor preservation. The root of the lateral incisor is round in cross section and smaller than that of the medial incisor; it is about the size of the root of P^2. The root of the medial incisor is elliptical in cross section and oriented obliquely to the other anterior teeth, indicating that it is probably the most anterior tooth. The front of the specimen is crushed, but there is some indication that the left premaxilla has been superimposed onto the right incisor region, thus strengthening the supposition that the medial incisor is indeed the most anterior tooth. The crowns of the upper incisors are not preserved. Szalay (1972b: fig. 1–9) recently referred an upper (?) incisor from Bear Creek tentatively to *C. nigridens*. Although it is superficially similar to that of archaic primates such as *Plesiadapis*, the incisor is probably referable to the plagiomenid *Planetetherium* (Rose, 1973); consequently, the crowns of the upper incisors of carpolestids remain unknown.

Carpolestes dubius Jepsen, 1930
Figures 5C, 24, 25, 27C, 27D, 29–31, 34E, 34F

Carpolestes dubius Jepsen, 1930: 520.

Holotype: PU 13275, right mandible with C, P_4-M_3, roots of I_1 and P_3, alveolus of I_2.

Hypodigm: Type and PU Nos. 13276, 13305 (Jepsen's "allotype"), 14069, 14077, 14235,

Figure 23. *Carpolestes nigridens* Simpson, holotype, AMNH 22159, right dentary with P_4–M_2. Crown view (above) and lateral view (below). × 6.

14341–14347, 17646, 17647, 17707–17710, 17856–17861, 17926, 17927, 17963, 19013, 19018, 19023, 19030, 19031, 19064, 19080, 19081, 19095, 19109, 19349, 19385, 19406, 19409, 19422, 19436, 19849, 19886, 21548, 21549; MCZ Nos. 19435–19438; all from Princeton Quarry level.

Horizon and Locality: latest Paleocene ("Clarkforkian"), Polecat Bench Formation of Wyoming: Bighorn Basin, including Princeton Quarry, Schaff Quarry, Fritz Quarry, and other nearby sites of approximately equivalent stratigraphic level.

Emended Diagnosis: P^3 with four prominent buccal cusps, anterior one slightly separated from three succeeding cusps; incipient fifth cusp at anteroexternal edge; anteroexternal projection much less elongate than in *C. nigridens*.

Discussion: As noted above, the only recognizable, consistent difference between this species and *C. nigridens* is in the morphology of P^3 (Figs. 27, 28). The incipient anterior buccal cusp arises from a faint anteroexternal cingulum in some individuals. It is this cusp which enlarges in *C. nigridens* to produce the anteroexternal "spur."

Jepsen (1930) presented a detailed description of *C. dubius* and outlined its distinctions from *C. nigridens*. The features he listed do differentiate between the type specimens of the two, but when series are examined, it becomes evident that none of the features occur consistently. Particularly variable are the prominence of vertical ridges and development of an internal cingulum on P_4, the height of the trigonid in M_1, and the development of the hypoconulid on M_1 and M_2. The tendency toward merging of the paraconid and metaconid on M_3 (as in the holotype and a few other individuals) seems to occur as a result of anteroposterior compression of the trigonid. However, the trigonid is compressed but otherwise normal in other individuals, so this is not a specific feature either. The dental formula accepted here (see diagnosis of *Carpolestes*) differs from Jepsen's interpretation (see discussion under *Elphidotarsius*, cf. *E. florencae*). Jepsen (1930:521) presumed that P^2 was two-rooted, but more complete material now available shows this to be a diminutive one-rooted tooth. He noted five cusps in the buccal row of P^3. As mentioned above, the most anterior of these is usually a small, incipient cusp; it is never as prominent as the other four cusps. This is the most important distinction between *C. dubius* and *C. nigridens;* and, in fact, Jepsen did point out that in P^3 of *C. dubius,* the anteroexternal projection is noticeably smaller than in the type of "*Litotherium complicatum*" (= *C. nigridens*).

Like the large sample of *Carpodaptes hazelae,* the sample now available for *Carpolestes dubius* offers an exceptional opportunity to observe the extent and kind of intraspecific variability which may occur in adult carpolestids. The population is essentially homogeneous in age; only adults are known (based on complete eruption of M^3_3 and absence of specimens preserving identified deciduous or erupting teeth), and very few could be considered senescent. As in other species of carpolestids, there are only minor variations in the molars, which, except for M_1, differ little even interspecifically throughout the family. The specialized premolars, P_4 and P^{3-4}, display much more variability.

Only one specimen (PU 14235) preserves the enlarged medial incisor (Figs. 5C, 24). It is similar to that in *Carpodaptes* in being more slender (laterally compressed) and longer than in *Elphidotarsius*. In *Carpolestes* the incisor is nearly twice as long from base to tip as in *Elphidotarsius*. Unlike *Elphidotarsius,* it does not broaden at the base of the crown, but is nearly as narrow (mesiodistally) there as at the tip. The ridge which formed the lateral (distal) border of the dorsal face of the incisor in *Elphidotarsius* has migrated mesially in *Carpolestes* to occupy a more central position on the dorsal aspect of the tooth. As a result, what was the dorsal face in *Elphidotarsius* now inclines sharply toward

Figure 24. Above: *Carpolestes dubius* Jepsen, PU 14235, left dentary with medial incisor, M_{1-2}, crown view. × 6. Below: *Carpolestes dubius* Jepsen, PU 19409, left dentary with C–M_3, medial view. × 6.

the midline in *Carpolestes*. At the base of the crown, the ridge meets a weakly-developed internal cingulum. The incisor is curved in two planes: dorsally at the tip of the crown (more so than in *Elphidotarsius*), and toward the midline at the tip. There are no evident wear facets on this incisor.

A few specimens preserve the reduced anterior teeth (I_2, C, P_3) which are all small, peglike, and single-rooted, as in *Carpodaptes hobackensis*. I_2 is often dis-

Figure 25. *Carpolestes dubius* Jepsen, PU 19409, left dentary with C–M_3. Crown view (above), lateral view (below). Schaff Quarry. × 6.

placed buccally (as deduced from the alveolus) in relation to the other anterior teeth (PU Nos. 17860, 19409). The enamel of the crown of the canine overhangs anteriorly but in P_3 this tendency is reduced (PU 17857) or lacking (PU 19409).

P_4 shows the greatest range of variation of any of the teeth. Size varies considerably

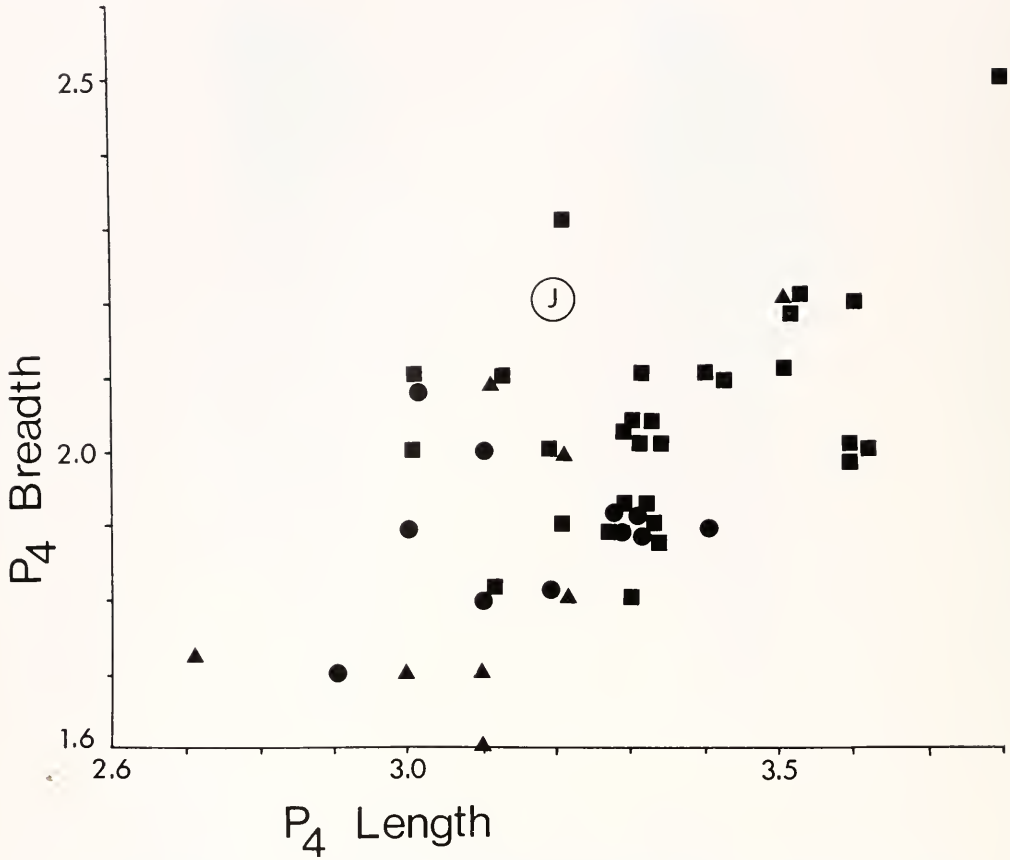


Figure 26. Scatter diagram of P_4 dimensions of *Carpolestes*. Black squares = *C. dubius*. Black circles = *C. nigridens*. Black triangles = *Carpolestes* sp. Circled J = *Carpodaptes jepseni*, holotype.

(see table). The apical cuspules may be sharp and distinct (PU Nos. 19409, 21549) or rather indistinct (holotype); their definition does not appear to be necessarily a function of the degree of wear. They are followed by a talonid cusp which smoothly continues the blade. There are usually eight apical cuspules, the eighth separated somewhat from the preceding seven and only slightly higher than the most anterior one. Some individuals show a faint indication of a ninth cuspule just anterior to the talonid (MCZ 19437). On the other hand, only seven apical cusps are present in PU 21549. The homologies of the apical cusps are not at all obvious, as they were in *Elphidotarsius*, but it is likely that proliferation of apical cuspules has occurred primarily at the front of P_4 (i.e., the original trigonid cusps are now situated at the end of the apical cusp sequence). A vertical ridge is present beneath each apical cusp on the lingual side. These ridges vary in distinction but are usually correlated with the degree of definition of the apical cusps. The ridge beneath the eighth cusp is always faint since this part of the tooth is concave, forming a posterointernal depression. This excavation is always present but is variable in depth. As noted above, the sinuous shape of the crest of P_4 (viewed occlusally) is due in part to this depression.

Vertical ridges may be present buccally as well, but are always much less distinct. Crown height of P_4 is variable, and like cusp definition, does not appear to be necessarily correlated with age or wear. P_4-M_3 are exodaenodont (see above, p. 11), particularly the buccal side of P_4. The enamel above the anterior root of P_4 extends lower than that above the posterior root in some individuals (PU 19409) a condition more pronounced lingually than buccally in PU 19886. In others (e.g. PU 19030) the enamel over the posterior root descends lower. The development of an internal cingulum on P_4 is variable. Some specimens, such as the holotype, have no internal cingulum (as noted by Jepsen, 1930). Jepsen apparently regarded the absence of an internal cingulum as a specific feature of *C. dubius,* but his paratype, PU 13284, has a weakly-expressed internal cingulum. It should be noted, however, that PU 13284 is recorded as coming from upper "Clarkforkian" beds, so it may represent *C. nigridens.* Other specimens that are undoubtedly associated with upper teeth referable to *C. dubius* have a basal cingulum extending across the entire lingual surface (PU Nos. 19031, 21549, MCZ 19438). The internal cingulum, when present, is usually better developed on the posterior half of the tooth (PU 17710, 19385). It may be developed anteriorly and posteriorly, but less so or not at all in the middle of the tooth (PU 17860). P_4 varies also in shape at the base of the crown (viewed occlusally). The shape is roughly quadrate but slightly laterally constricted at the midsection (between the roots). In some specimens, the posterior half of the tooth is more laterally compressed than the anterior half (PU 19409); in others the anterior half is more compressed (PU 17861). Some specimens of P_4 are relatively quite narrow buccolingually (PU 17861). These features have been cited to illustrate the exceptional variability of P_4 in *C. dubius.* Although most other samples of carpolestid species are considerably smaller, it appears that similar variation is typical of carpolestids in general.

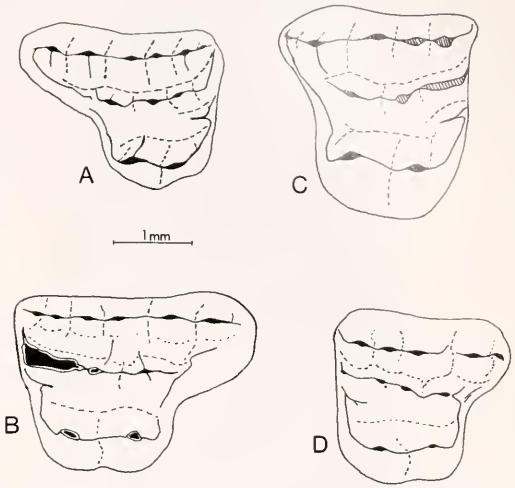


Figure 27. Comparison of P^3 in *Carpolestes,* to same scale. *C. nigridens*: A) PU 19543, left P^3; B) YPM 24614, right P^3. *C. dubius*: C) PU 19349, left P^3; D) PU 14077, right P^3.

The lower molars of *C. dubius* are much less variable than P_4. Variation in size is not so apparent as in P_4. A faint external cingulum develops on the molars of some individuals, but it is never very distinct and is often absent. A weak internal cingulum may develop on the trigonid of M_1 (holotype and PU 17710), but this, too, is often absent. The trigonid of M_1 and the talonid of P_4 are invariably the same height. (In PU 19409 [see Figs. 24, 25] the talonid of P_4 appears to be lower than the trigonid of M_1; this is due to breakage and subsequent distortion of this specimen.) The posterior edge of P_4 and the anterior edge of M_1 are compacted, forming a continuous blade from the anterior edge of P_4 to the protoconid of M_1.

At least fifteen specimens of upper dentitions (see Figs. 29, 30, 34F) are referable to *C. dubius,* more than are known in any other carpolestid. The most anterior tooth known is the diminutive P^2. As aforementioned, Jepsen (1930) thought P^2 was two-rooted, but specimens now known (PU

TABLE 5. METRICAL DATA FOR LOWER CHEEK TEETH OF *CARPOLESTES DUBIUS* FROM PRINCETON QUARRY LEVEL.

		N	OR (mm)	$\bar{x}$	s	V
P_4	length	26	3.0–3.6	3.32 ± .03	.172 ± .024	5.2 ± .7
	breadth	27	1.8–2.3	2.01 ± .02	.120 ± .016	6.0 ± .8
M_1	length	23	1.6–2.0	1.87 ± .02	.105 ± .015	5.6 ± .8
	breadth	23	1.5–2.1	1.67 ± .03	.150 ± .022	9.0 ± 1.3
M_2	length	15	1.4–1.7	1.54 ± .02	.074 ± .014	4.8 ± .9
	breadth	15	1.4–1.7	1.54 ± .02	.074 ± .014	4.8 ± .9
M_3	length	6	2.0–2.3	2.13 ± .05	.121 ± .035	5.7 ± 1.6
	breadth	6	1.3–1.4	1.38 ± .02	.041 ± .012	3.0 ± .9
Mandibular depth		7	4.0–5.5	4.87 ± .18	.489 ± .131	10.0 ± 2.7

Nos. 19349, 19422) reveal that it is a one-rooted tooth with one main cusp. A cingulum, faint buccally but well developed lingually, surrounds it; this rises at the anterior and posterior edges of the tooth, posteriorly giving the suggestion of a small second cusp.

Little can be added to Jepsen's (1930: 521–522) accurate and detailed description of P^3 and P^4. Compared to P_4, the morphology of P^3 and P^4 is relatively constant. Jepsen described P^3 as having five cusps in the external row, but as already noted, the first of these is incipient and never approaches the magnitude achieved in *C. nigridens*. In PU 13305, on which Jepsen based his description, this cusp is larger than in most other specimens. The cusp is represented only by a slight rise of the anteroexternal cingulum in some others

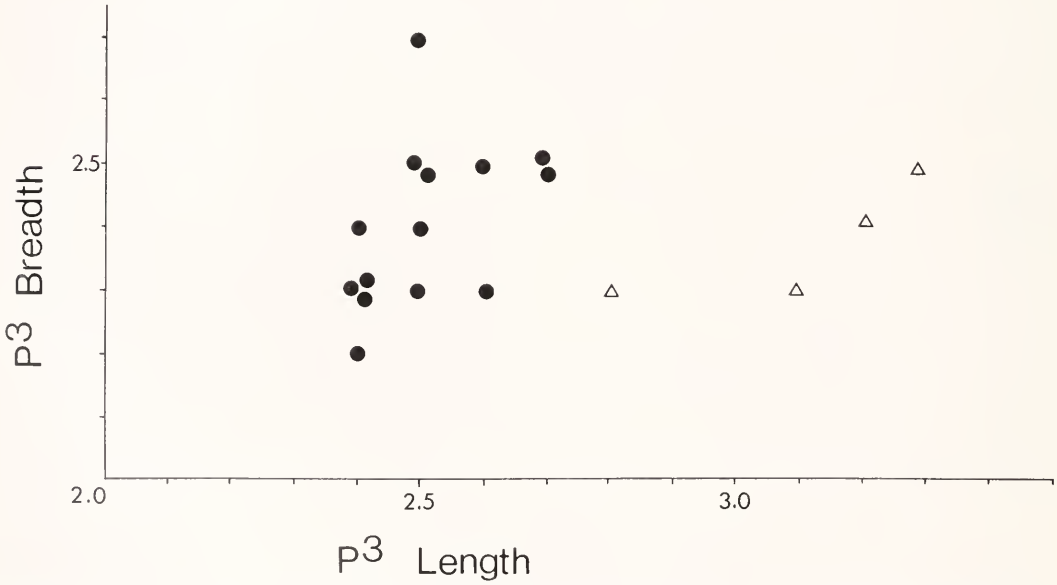


Figure 28. Scatter diagram of P^3 dimensions of *Carpolestes*. Black circles = *C. dubius*. Open triangles = *C. nigridens*.

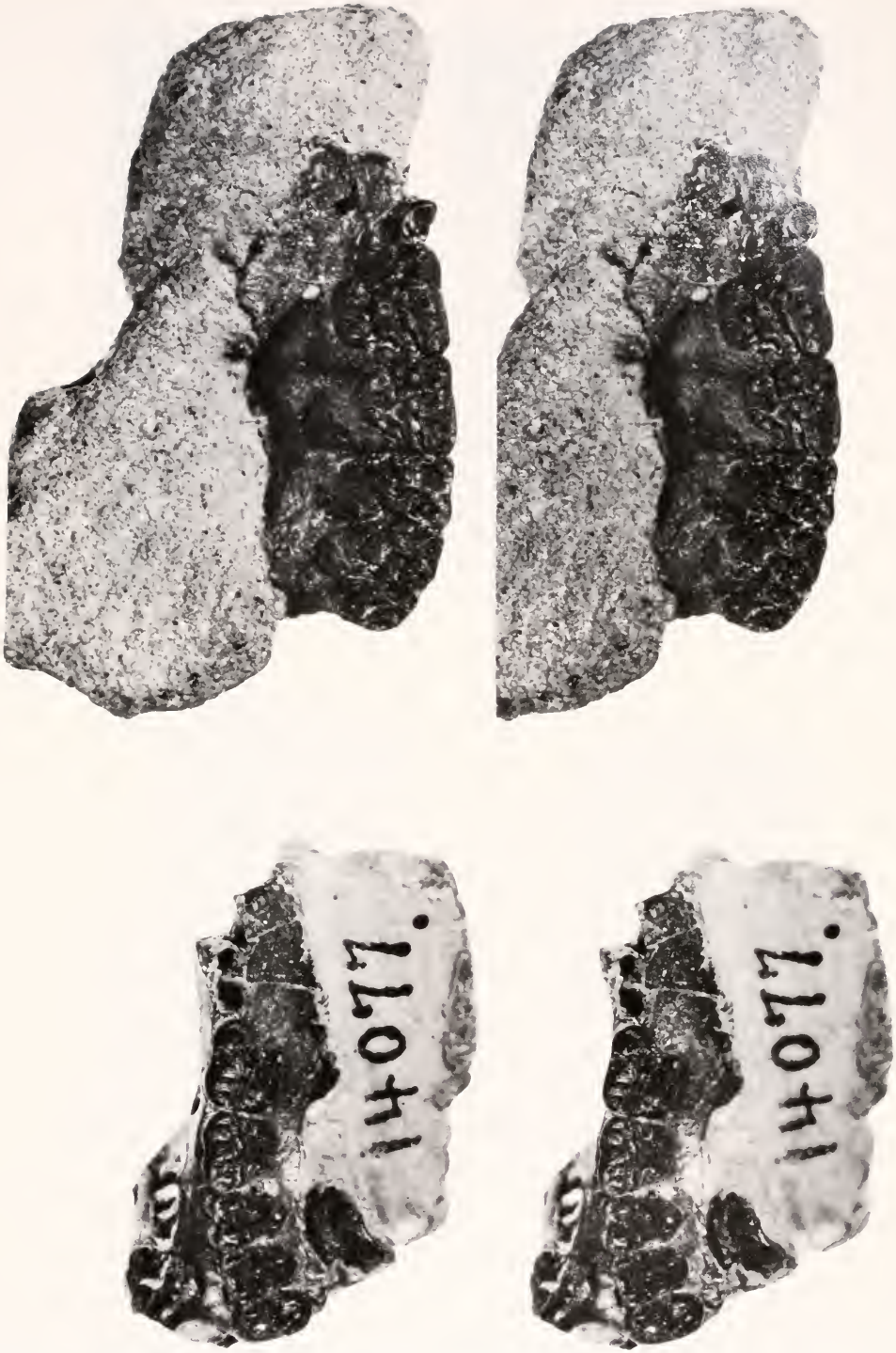


Figure 29. *Carpolestes dubius* Jepsen. Above: PU 19349, left maxilla with P^2–M^3, crown view. Below: PU 14077, right maxilla with P^3–M^3, crown view. × 6.

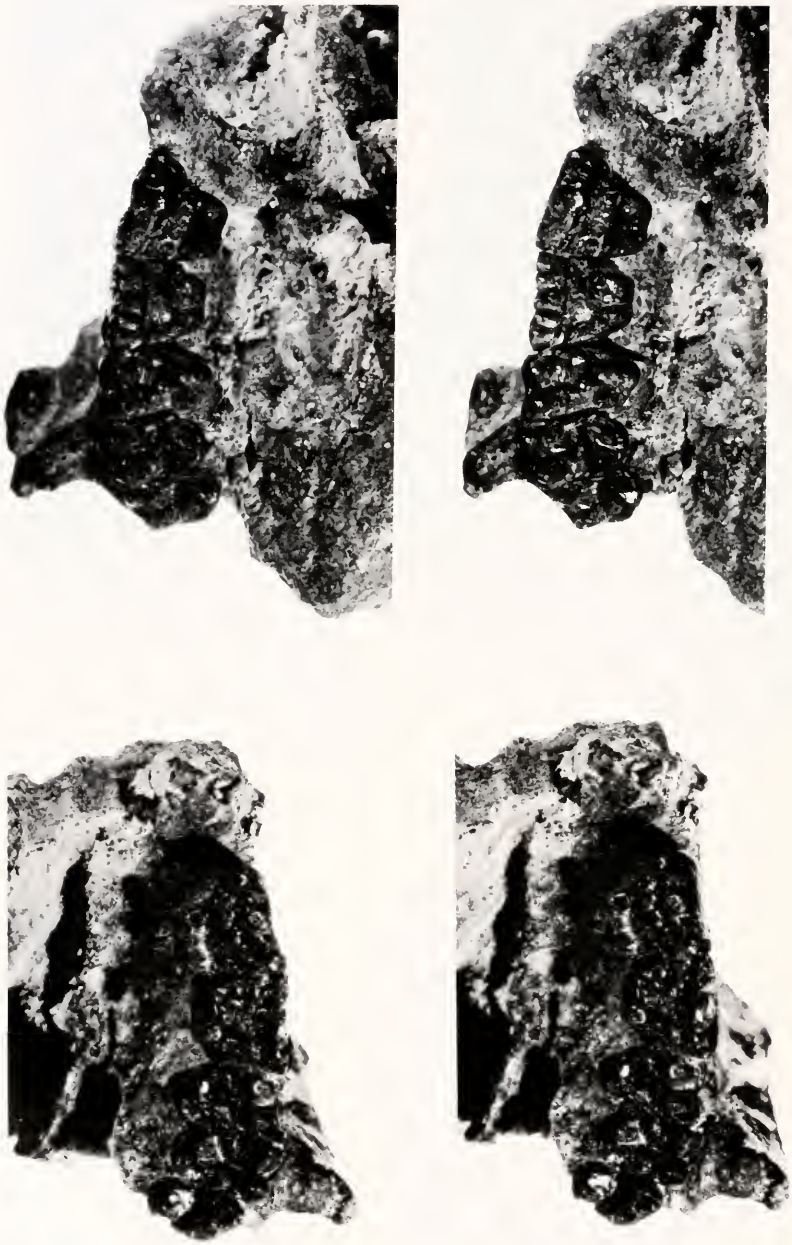


Figure 30. *Carpolestes dubius* Jepsen, PU 17709, palate. Above: right P^3–M^3, crown view. × 6. Below: left P^3–M^3, crown view. × 6.

(PU 17709, 19439), suggesting that it originated as a stylar cusp. P^4 may show a small sixth cusp at the posterior end of the external cusp row (PU 17709). The cusps of the medial row in both P^3 and P^4 are difficult to distinguish; this row in both teeth is more of a "rugose crest", as noted by Jepsen. In P^3 the anterior part of this

TABLE 6. METRICAL DATA FOR UPPER CHEEK TEETH OF *CARPOLESTES DUBIUS* FROM PRINCETON QUARRY LEVEL.

		N	OR (mm)	$\bar{x}$	s	V
P^3	length	14	2.4–2.7	2.51 ± .03	.107 ± .020	4.3 ± .8
	breadth	14	2.2–2.7	2.41 ± .04	.133 ± .025	5.5 ± 1.0
P^4	length	12	2.0–2.4	2.23 ± .03	.087 ± .018	3.9 ± .8
	breadth	13	1.9–2.5	2.17 ± .04	.144 ± .028	6.6 ± 1.3
M^1	length	9	1.5–1.8	1.58 ± .03	.097 ± .023	6.2 ± 1.5
	breadth	9	2.1–2.5	2.27 ± .05	.158 ± .037	7.0 ± 1.6
M^2	length	8	1.4–1.5	1.49 ± .01	.035 ± .009	2.4 ± .6
	breadth	8	2.0–2.3	2.19 ± .05	.136 ± .034	6.2 ± 1.6
M^3	length	6	1.3–1.4	1.32 ± .02	.041 ± .012	3.1 ± .9
	breadth	6	1.9–2.2	2.02 ± .04	.098 ± .028	4.9 ± 1.4

crest bears a distinct, well-developed cusp, and wear patterns suggest the presence of perhaps three additional cusps on this crest (PU 19349). In P^4 the only recognizable cusp on the medial crest is approximately at the center of the crest. A faint external cingulum may develop posteriorly on P^4. The enamel of both P^3 and P^4 is crenulated, particularly on the buccal side of each tooth and on the lingual faces of the external and medial cusp rows. P^3 is always larger—both broader and longer—than P^4.

A strong external cingulum is present on the molars. Stylar cusps are extremely faint, if present at all. An incipient parastyle is present in several specimens, and a small mesostyle can be detected on M^1 of PU 19349. Anterior and posterior cingula are usually present but less developed than the external cingulum. A faint internal cingulum may unite the anterior and posterior cingula (PU 17709). The hypocone, originating from the posterior cingulum, is usually well expressed, although decreasing in size posteriorly. The anterior cingulum in some individuals (PU 19349) gives rise to a vague, incipient pericone (referred to by Jepsen [1930: 522] as an ectocone); this is rarely detectable except on M^1.

One specimen (PU 19422, a snout with most of the palatal dentition, see Fig. 31) bears an anomalous small right M^1 (left M^1 is normal). The anomalous tooth is much narrower buccolingually than the other molars, its paracone and metacone aligning with the conules of M^2 and M^3. It lacks a hypocone. The paraconule is well developed, but the metaconule is indistinct. This morphology is strikingly similar to that of dP^4 of *Plesiadapis* (Simpson, 1935a: 6). The presence in PU 19422 of the fully erupted, complete adult dentition, including right and left P^3, P^4, and M^3, seems to preclude any possibility that this represents a deciduous tooth, however.

When *Carpolestes dubius* was described, PU 13305 was the only known maxillary fragment. Although several more specimens are now available, only a few add to our knowledge of palatal and skull anatomy. A partially crushed snout (PU 19422, see Figs. 31 and 32) reveals several details, but much of the structure remains vague as a result of post mortem distortion and the exceptionally hard matrix. The features discussed below are based primarily on this specimen, supplemented by evidence provided from PU Nos. 17709 (a partial palate), 13305, 14077, and 17927.

The maxillae contribute significantly to the face, apparently relatively more so than in *Plesiadapis*. A large infraorbital foramen opens above the posterior root of P^3, or more often slightly posterior to that point. As noted by Jepsen (1930), the jugal process

Figure 31. *Carpolestes dubius* Jepsen, PU 19422, snout. Left: palatal view. Right: crown view, right maxillary dentition including P^{3-4} and anomalous M^1. × 6.

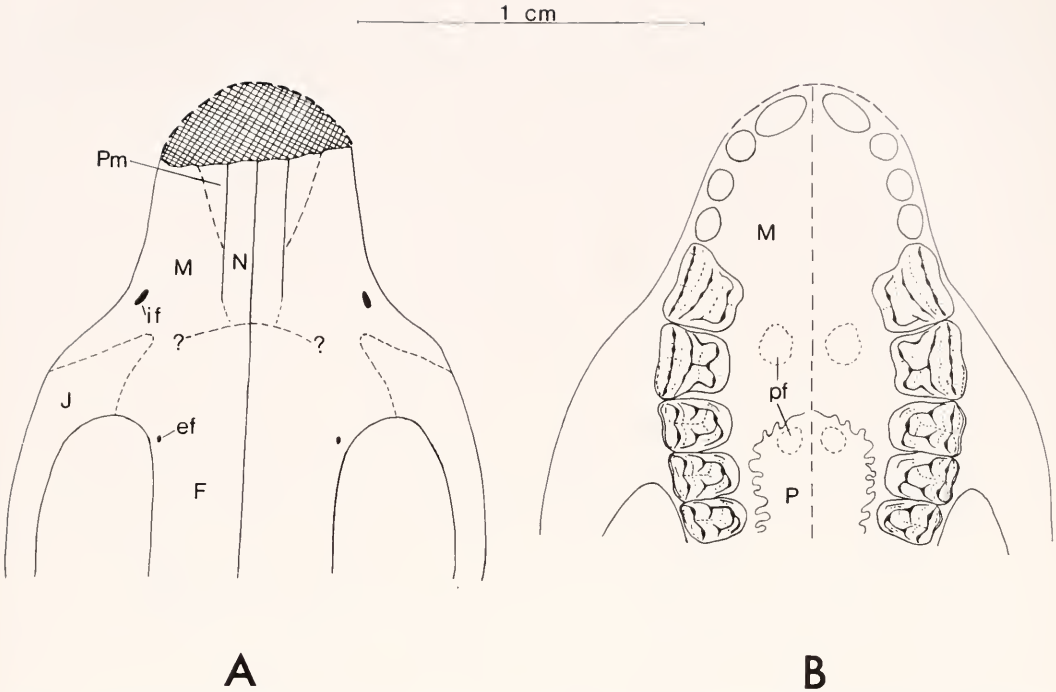


Figure 32. Tentative reconstructions of A) snout, and B) palate of *Carpolestes*, based primarily on PU Nos. 19422, 17709, 17978, and 13305. ef = emissary foramen. F = frontal. if = infraorbital foramen. J = jugal. M = maxilla. N = nasal. P = palatine. pf = palatal fenestrae. Pm = premaxilla.

of the maxilla emerges approximately above M^2. The jugal portion of the zygomatic arch is preserved in PU 19422 and is robust, as in *Plesiadapis*. The suture between the maxilla and the jugal is nearly horizontal (but slightly more dorsal anteriorly) and extends approximately from above M^2 to above the anterior part of P^4. Matrix obscures the extent of the lacrimal. The premaxillae, missing anteriorly in PU 19422, are relatively small, contrasting markedly with *Plesiadapis* (Russell, 1959, 1964), where they are very large and form a major part of the snout. A small (emissary?) foramen is present anterolaterally in each frontal, near but just outside the orbital margin.

Jepsen (1930) has noted the peculiar palatal fenestrae in this species. The new material collected since his description unfortunately does not reveal more precisely the position or extent of these fenestrae. Their occurrence in carpolestids is unique among primates, and their function is unclear. One pair was situated approximately internal to P^3, bounded at least laterally by the maxillae. There is some indication of a more posterior pair which may or may not have been connected with the anterior pair. These are internal to M^1 or M^2 and appear to be within the palatine; they may possibly be enlarged posterior palatine foramina.

The specimens here referred to *C. dubius* are all from Princeton Quarry and nearby sites of equivalent stratigraphic level, and only specimens from this earliest "Clarkforkian" horizon are included in the hypodigm. All referred lower dentitions are from localities at which they are associated with maxillary dentitions containing P^3 diagnostic of *C. dubius*. P^3 with *C. nigridens* morphology has not been found at this horizon. Separation of the two species

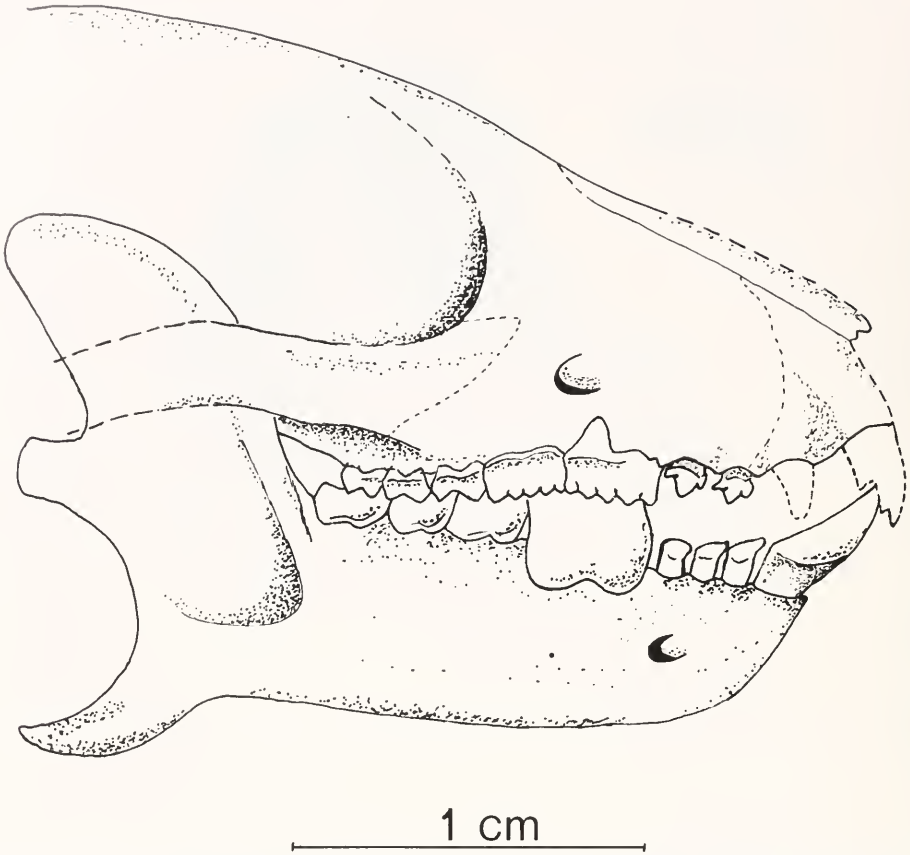


Figure 33. Tentative reconstruction of the skull of *Carpolestes*, based on PU Nos. 14235, 19409, 19422, 14077, 17978, and 19349. Angular process of mandible restored from PU 21399 (*Carpodaptes hazelae*); upper canine restored from AMNH 33980 (*Carpodaptes hazelae*).

on stratigraphic criteria eventually may prove justifiable, but is precarious at present.

C. dubius is surely the immediate ancestor of *C. nigridens*. Future discoveries may reveal that P^3 morphology is variable and not taxonomically significant, and that *C. dubius* should be placed in synonymy. As long as the two species are maintained, however, mandibular dentitions of *Carpolestes* will be assignable to species only if associated with P^3. Consequently, about a dozen specimens, including those from Buckman Hollow (USNM 21280) and Togwotee Pass (AMNH 88198), and several from the Big Horn Basin, must, for the present, be referred to *Carpolestes*, species indeterminate.

A tentative reconstruction of the skull of *Carpolestes*, based primarily on specimens of *C. dubius*, is presented in Figure 33.

The Phyletic Position of *Saxonella*

D. E. Russell (1964) described *Saxonella crepaturae*, from the Middle Paleocene of Walbeck, Germany, and referred it to the Carpolestidae. Differences between the new form and the North American carpolestids compelled Russell to propose two subfamilies, the Carpolestinae, for the North American genera, and the Saxonel-

linae, for the new genus. Like the North American forms, *Saxonella* has a "plagiaulacoid" dental complex in the mandible, but the premolar specialization is not the same as in carpolestids. In *Saxonella*, P_3 is enlarged and trenchant and P_4 relatively small. Such a difference is fundamental and precludes the possibility of very close relationship between *Saxonella* and carpolestids. Furthermore, the mandibular dental formula, 1.0.2.3, is reduced beyond that in even the most advanced carpolestids, although *Saxonella* appears to have been contemporary with the earliest known North American species of the family.

Russell's assignment of *Saxonella* to the Carpolestidae was, nevertheless, accepted by some authors (e.g., Romer, 1966; McKenna, 1967).

Some features (e.g., molar and incisor morphology, form of $?P^4$, and mandibular dental formula) are equally or more suggestive of plesiadapid affinities, although the dental reduction in *Saxonella* exceeds even that in contemporary plesiadapids. Moreover, Russell was surely correct in suggesting that other early primates had upper incisors of comparable structure. Van Valen (1969) formally transferred *Saxonella* from the Carpolestidae to the Plesiadapidae, a view followed by Szalay (1970, 1972b), Simons (1972), and Butler (1973).

The morphology of *Saxonella* points to affinities with both carpolestids and plesiadapids, but its specializations are comparable in magnitude, although different from, those of either family. Accordingly, *Saxonella* should be separated from both at the family level, as the Saxonellidae, but grouped with them in the superfamily Plesiadapoidea.

MORPHOLOGY AND FUNCTION

The "Plagiaulacoid" Dentition

The lower dentition in carpolestids is characterized by a hypertrophied, trenchant P_4, an enlarged medial incisor, and reduced dentition between these, a pattern termed "plagiaulacoid" (Abel, 1931; Simpson, 1933) in allusion to its occurrence in members of the multituberculate suborder Plagiaulacoidea. The complex is present in several other mammalian groups, including ptilodontoid multituberculates, caenolestoid marsupials (Simpson, 1933; Paula Couto, 1952), phalangeroid marsupials, and the plesiadapoid *Saxonella*. Simpson (1933) concluded that plagiaulacoidy was acquired independently at least four times: probably once in multituberculates, twice or more in marsupials, and once in primates (*Saxonella* then being unknown). The differing homologies of the sectorial tooth in *Saxonella* and carpolestids make it virtually certain that two independent origins occurred in primates.

The bladelike specialization in these mammals may involve more than one tooth, as in plagiaulacids such as *Ctenacodon*, but is usually restricted to one. In the latter case it is not always the same tooth: in *Saxonella* it is P_3, not P_4 as in carpolestids; in caenolestoids it is P_3 or M_1, and in Australian marsupials it is P_3 (the last premolar). In ptilodontid multituberculates the blade has generally been assumed to be P_4, but there is some evidence to suggest that it is actually the first molar (Bohlin, 1945; Sloan, Kielan-Jaworowska, personal communication).

The adaptive significance of the "plagiaulacoid" dentition may be generally similar in the varied types possessing it, but dissimilar upper dentitions in most of these mammals suggest that the function is variable. Simpson (1933) concluded that it is an adaptation for herbivory, especially efficient for dealing with coarse vegetation.

The only extant mammals with the "plagiaulacoid" dentition are certain macropodid marsupials (e.g., *Hypsiprymnodon, Dorcopsis, Aepyprymnus, Bettongia*) and the phalangerid *Burramys*, Australian forms in which the sectorial lower tooth is opposed by a similar trenchant tooth in the upper jaw. This complex is quite different from that in carpolestids, and inferences of

carpolestid dental function or diet by analogy with these "plagiaulacoid" marsupials are probably poorly founded. Furthermore, although most of these marsupials feed on vegetation such as fruits, berries, and leaves, at least one form (*Hypsiprymnodon*) is known to ingest substantial quantities of insects and worms (Walker et al., 1968). Simpson (1933) contrasted the unusual upper premolars of *Carpolestes* with the upper teeth of other "plagiaulacoid" mammals and speculated that carpolestids may have been more frugivorous than extant "plagiaulacoid" marsupials.

The upper premolars of some ptilodontoid multituberculates show superficial similarities to those of advanced carpolestids, but there are indications that multituberculate dentitions functioned differently than those of carpolestids. Almost certainly the sectorial lower tooth of multituberculates was more directly involved with powerful shearing than appears to have been the case in carpolestids.[1] Carpolestids and multituberculates may have been to some extent mutually competitive, but dental resemblances between the two may indicate only that both were specialized herbivores.

The upper teeth of *Saxonella* are less specialized than those of *Carpodaptes* and *Carpolestes,* but not unlike those of *Elphidotarsius;* and it may be postulated that dental function in *Elphidotarsius* and *Saxonella* was similar.

Major Features and Trends in the Carpolestid Dentition and Skull

The lower dental formula is $\overline{2.1.3.3}$ in *Elphidotarsius* and $\overline{2.1.2.3.}$ in *Carpodaptes* and *Carpolestes. Elphidotarsius* has many similarities to the contemporary plesiadapid *Pronothodectes,* but its P_4, enlarged and bladelike, is characteristically carpolestid. It retains three lower premolars, like *Pronothodectes.* P_2, judging from its alveolus, was a small, single-rooted, peglike tooth. P_3 is small relative to P_4 but is comparatively unreduced and premolariform. In *Carpodaptes* and *Carpolestes,* the mandibular dentition is similar to that of *Elphidotarsius,* but further specialization and hypertrophy of P_4 has resulted in the loss of P_2 and the simplification of P_3 into a single-rooted peg.

Upper dentitions of carpolestids (Fig. 34), as for many other fossil mammals, are much less well represented in collections than are mandibles. Upper teeth or partial dentitions are known for *Elphidotarsius* cf. *florencae, Carpodaptes hazelae, C. cygneus, Carpolestes nigridens,* and *C. dubius,* the latter species being the best known. The most anterior upper teeth are unknown in *Elphidotarsius* and *Carpodaptes.* Specimens of *Carpolestes* suggest an upper dental formula of $\overline{2.1.3.3}$ in this genus. The maxillary-premaxillary suture is poorly preserved and unclear in all specimens preserving this region, but its apparent position is consistent with the interpretation of the dental formula given here.

A number of features of carpolestids observed to be more fully developed in the later, more specialized species may be regarded as trends. For example, size tends to increase through time. *Carpodaptes* is generally larger than *Elphidotarsius,* and *Carpolestes* is always larger than all but one of the species (*Carpodaptes jepseni*) of the other two genera. While this trend involves primarily the cheek teeth, P_4 and P^{3-4} are particularly affected. Some exceptions have already been noted: *Carpodaptes hobackensis* and *C. cygneus* are smaller than the known species of *Elphidotarsius* and may be representative of a side branch of the genus which was decreasing in size; *Carpodaptes jepseni* is fully as large as *Carpolestes.* Correlated with the gradual

[1] Hahn (1971) illustrated teeth of the Upper Jurassic paulchoffatiid multituberculates that demonstrate that their premolars were not involved in shearing; they show considerable abrasive wear and erosion at the apices of the cusps, somewhat as in carpolestid premolars (see below).

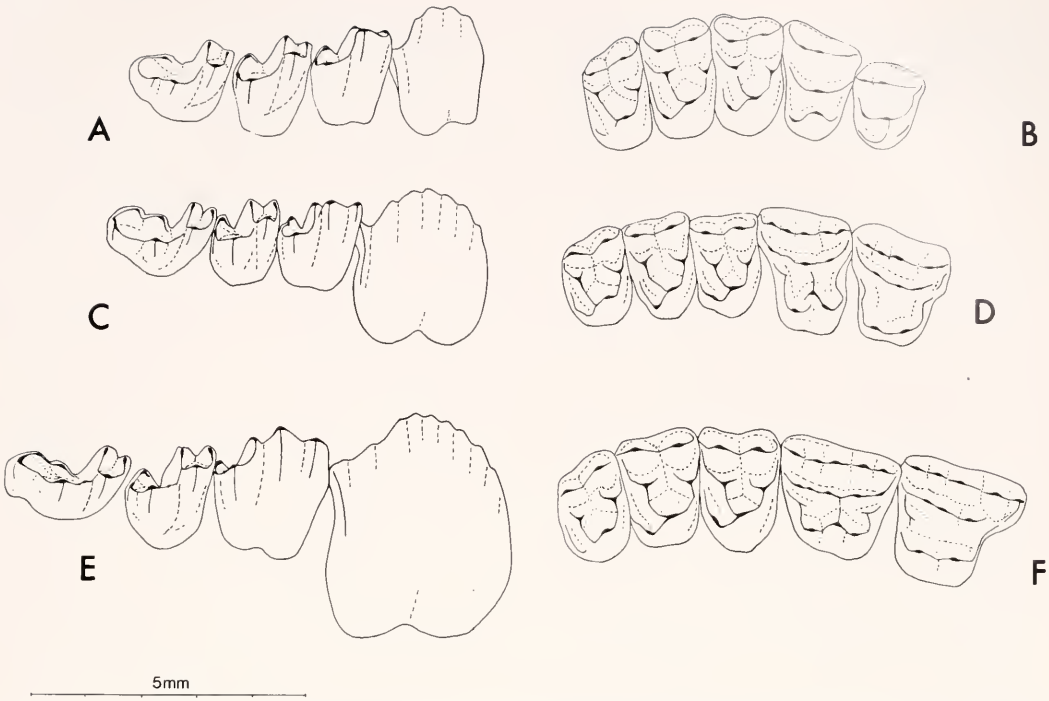


Figure 34. Lower cheek teeth (P_4–M_3) and upper cheek teeth (P^3–M^3) of carpolestids, to same scale. A and B) *Elphidotarsius* (based on *E.*, cf. *E. florencae*). C and D) *Carpodaptes* (based on *C. hazelae*). E and F) *Carpolestes* (based on *C. dubius*).

increase in size of the teeth is increasing mandibular depth to accommodate the lengthening roots, particularly of P_4. The mandible of *Elphidotarsius* is relatively shallow (2.8–3.5 mm); that of *Carpodaptes* is somewhat deeper (3.1–4.0 mm; 5.5 mm in *C. jepseni*); and the jaw of *Carpolestes* is comparatively deep (4.0–5.5 mm). There is also a trend toward lengthening and slenderizing the enlarged medial incisor.

Associated with size increase is the increasing specialization of P_4 and P^{3-4} (see Fig. 34). The enlargement and specialization of these teeth occurred, at least in part, at the expense of the anterior teeth (except the medial incisors), which underwent reduction through time. Specialization was accomplished by the addition of accessory cusps, with the result that in the two more specialized genera cusp homologies are not entirely clear. As in most Paleocene primates, the antemolar modifications are more diagnostic than are the molars, which remain relatively conservative (paromomyids such as *Phenacolemur* and *Micromomys* [Szalay, 1973] have an enlarged P_4, reduced anterior teeth except the incisor, and relatively conservative molars).

Specialization of P_4 in carpolestids was accompanied by elongation of the trigonid of M_1. The trigonid cusps of M_1 in *Elphidotarsius* are arranged in a triangle, but in *Carpodaptes* and *Carpolestes* the paraconid and protoconid are drawn out, nearly or exactly in line, and colinear with the cusps of P_4. The lengthening of the trigonid of M_1 occurs at the expense of the length of the talonid and is relatively more marked in *Carpolestes* than in *Carpodaptes*.

M_3 tends to enlarge in the sequence *Elphidotarsius-Carpodaptes-Carpolestes*, par-

ticularly by elongation of the third lobe. The hypoconulid of M_3 is typically twinned, and there is often a small mesoconid on the cristid obliqua in later forms. Breadth of P_4 and of the lower molars shows a tendency to increase through time, but this feature is among the most variable intraspecifically and hence of little taxonomic value.

The clearest trend in the upper dentition, as noted above, is toward specialization and hypertrophy of P^{3-4} (associated with the enlargement of P_4). In *Elphidotarsius,* these teeth are smaller than the molars (or P_4 may be about the size of the molars), but in *Carpodaptes* and *Carpolestes* they are noticeably larger than the molars. P^3 changes the most. It is a small, relatively generalized, premolariform tooth in *Elphidotarsius.* In *Carpodaptes* it is already subequal to P^4, while in *Carpolestes* it is always larger than P^4 and may display a conspicuous anteroexternal projection. P^4 is somewhat specialized in *Elphidotarsius,* already at this stage longitudinally tripartite. These three sections are much more complex in *Carpodaptes* and *Carpolestes.* The latter two genera have a closely similar P^4, the main distinction being the greater anteroposterior length in *Carpolestes.* Both P^3 and P^4 in the two later genera are polycuspate, with numerous accessory cusps.

Intraspecific variability of the teeth has been discussed in the systematics section. The much larger samples of carpolestids now available provide a reasonably adequate basis for concluding, as did Butler (1963: 1), that "paleontologists have tended to underestimate the variability of fossil species."

It should be noted that all known specimens of carpolestids, as far as can be determined, represent adult individuals. In no specimen is there evidence of deciduous or erupting teeth, and those preserving the posterior part of the jaw always reveal a fully erupted M_3 (or its alveolus). Only a small number of individuals are in advanced stages of wear.

The most conspicuous trend in mandibular morphology is increasing depth, associated with the lengthening of the roots of P_4. The mental foramen is variable in position beneath P_2 or P_3 in *Elphidotarsius* and below $\overline{C}$ or P_3 in *Carpodaptes* and *Carpolestes.* As in most prosimians, the symphysis was unfused in carpolestids. The posterior part of the mandible is preserved in near entirety only in a few specimens of *Carpodaptes hazelae* (PU 20615, 21341, 21399; see Fig. 35). It is closely comparable to the back of the dentary in *Plesiadapis* (PU 21246). The coronoid process is high and broad. The angular process is recurved and tapers posteriorly, forming a hooklike process much like the angle in other archaic primates such as *Plesiadapis* and *Phenacolemur,* and in such Recent insectivorans as *Ptilocercus, Setifer,* and *Neotetragus.* It serves as a point of insertion for the internal pterygoid and part of the masseter. The condyle in *Carpodaptes,* as in *Plesiadapis,* is situated about midway between the angular process and the top of the coronoid, about even with or just slightly above the tooth row. In *Phenacolemur* (PU 21405) the condyle is markedly higher than the tooth row. (This feature, together with dental morphology, suggests that *Phenacolemur* may have been more strictly herbivorous than either *Plesiadapis* or the carpolestids.) The articular surface of the condyle, well preserved in only one specimen (PU 21399), covers the entire dorsal and posterior surfaces of the condyle; its transverse diameter is approximately 1.6 mm.

The few known details about the palate and front of the skull are based primarily on specimens of *Carpolestes dubius* and have been discussed under that species in the section on systematics. Skulls of archaic primates are poorly known. Only that of *Plesiadapis* is reasonably well preserved (Russell, 1959, 1964). *Phenacolemur* (Simpson, 1955; Szalay, 1972a) and *Palaechthon*

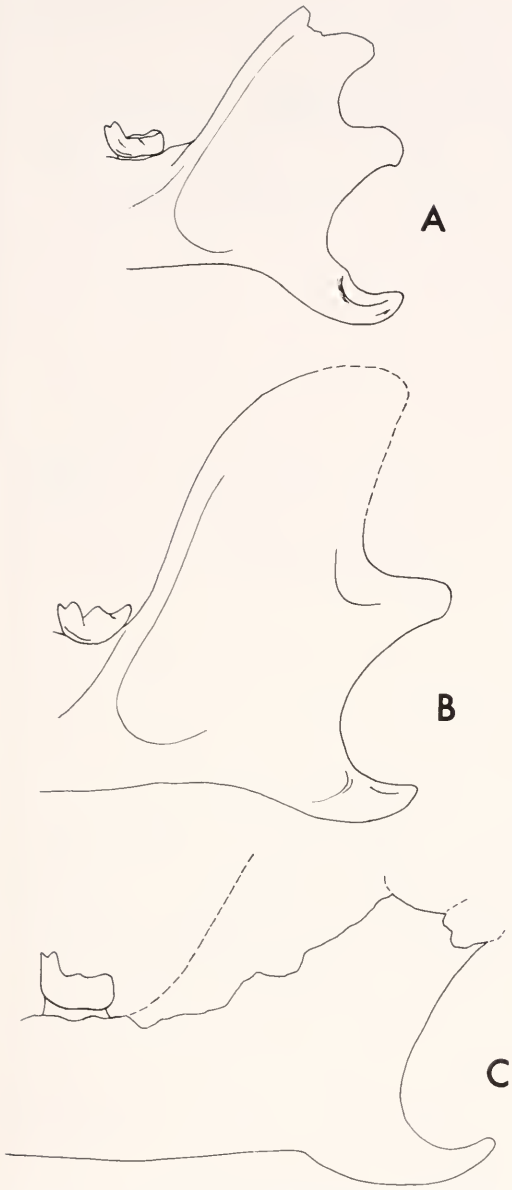


Figure 35. Lateral view of posterior of mandible, not to same scale. A) *Carpodaptes hazelae*, PU 21399. B) *Plesiadapis rex*, PU 21246 (reversed). C) *Phenacolemur* sp., PU 21405 (M_3 restored).

(Wilson and Szalay, 1972) are each known from one poorly preserved skull. Present evidence permits few comparisons between *Carpolestes* and these genera, but it is probably valid to conclude that the palatal (and preorbital) length was relatively much less in *Carpolestes* than in *Plesiadapis,* and was comparable to or slightly less than in *Palaechthon.*

Occlusion and Dental Function

Introduction. Recent cineradiographic studies of living mammals have provided much information on the movement of the mandible and the function of the teeth during feeding (e.g. Ardran et al., 1958; Crompton and Hiiemäe, 1970; Hiiemäe and Ardran, 1968; Hiiemäe and Crompton, 1971; Hiiemäe and Kay, 1972, 1973; Kay and Hiiemäe, 1974a, b; Ride, 1959). For example, it has been established that in the opossum, *Didelphis,* feeding involves four steps: ingestion, transfer of food to the molar region, mastication, and deglutition, sometimes including regurgitation for further preparation by the teeth (Hiiemäe and Crompton, 1971). Mastication, the step involving preparation of the food by the cheek teeth, can be separated into three components: the upstroke or preparatory stroke, the power stroke (occlusal or near occlusal stroke), and the downstroke or recovery stroke (Hiiemäe, 1967; Hiiemäe and Ardran, 1968; Crompton and Hiiemäe, 1969a, 1970; Hiiemäe and Crompton, 1971; Kay and Hiiemäe, 1974a, b).

Two stages of mastication have been observed. The first, a puncture-crushing stage involving no direct contact of the upper and lower teeth causes wear on the tips of the cusps, resulting eventually in exposure of the dentine through windows in the enamel. The term "abrasion" has been used to describe wear resulting from the puncture-crushing stage of mastication (Hiiemäe and Kay, 1973; Kay and Hiiemäe, 1974a). Gingerich observed striated wear facets on the posterior surface of the metacone and anterior surface of the protoconid in *Adapis* (Gingerich, 1972) and on the front of the main cusp of P_4 in *Phenacolemur* (Gingerich, 1974a). He believes this wear to be a result of "orthal retrac-

tion", which took place during the puncture-crushing stage.

The second stage of mastication is direct tooth-to-tooth occlusion during which shearing, crushing, and often grinding[1] occurs (Crompton and Hiiemäe, 1970; Kay and Hiiemäe, 1974a). This results in striated wear facets on the crests which join the cusps of the teeth, and in the basins. The resulting wear has been called "attrition" (Kay and Hiiemäe, 1974b). A number of recent investigations have made use of these facets in interpretations of the function of molariform teeth in therian mammals (e.g., Butler, 1952, 1972, 1973; Crompton, 1971; Crompton and Hiiemäe, 1969a, b, 1970; Gingerich, 1972, and in press; Hiiemäe and Kay, 1973; Kay and Hiiemäe, 1974b; Mills, 1955, 1966, 1967).

The power stroke of the occlusal stage of mastication in primates has two components, each forming a set of matching occlusal wear facets on the upper and lower teeth. Mills (1955, 1967) has used the terms "buccal phase" and "lingual phase" to describe the movement of the mandible during the power stroke, and the resultant wear facets. According to him, the buccal phase on the active side coincides with the lingual phase on the opposite side, promoting balanced occlusion (and simultaneously formed buccal and lingual phase facets). Hiiemäe and Kay (1972, 1973; and Kay and Hiiemäe, 1974b), on the other hand, have shown convincingly that no such balanced occlusion occurs in the primates they studied cinefluorographically. Wear facets thus reflect successive phases of the power stroke on the same side of the jaw. Because buccal phase and lingual phase, as defined by Mills (1955), differ from observed mandibular movements and methods of formation of wear facets, Hiiemäe and Kay (1972) have proposed the terms "Phase I" and "Phase II" to describe the successive phases of the power stroke. During Phase I in primates, the active side of the mandible moves upward, medially, and slightly anteriorly, until the teeth are in centric occlusion. The facets produced face buccally on the lower teeth, lingually on the uppers. In Phase II, the active side moves downward and further medially and anteriorly (in such forms as *Ptilocercus* and *Erinaceus* the jaws moves posteromedially, rather than anteromedially, during Phase II [Mills, 1967]). Phase II facets face lingually on the lower teeth, buccally on the uppers. This phase involves a slight shift in direction from that of Phase I, which is reflected in a difference in the direction of Phase I and Phase II facets. However, wear facets with striations intermediate in direction between those of Phase I and Phase II have been observed in *Plesiadapis*, suggesting that the two phases in this form were parts of a single, transverse movement (Gingerich, in press).

Carpolestids. Phase I and Phase II facets have been observed on upper and lower molars of carpolestids and are mapped in Figures 36–38. Facets have been numbered according to the scheme introduced by Crompton (1971) and followed by Gingerich (in press) and Kay and Hiiemäe (1974a). Facets 1–7 are formed during Phase I, facets 9 and 10 during Phase II. Occluding wear surfaces on upper and lower teeth are given the same number. Molar function in all three genera of carpolestids was very similar to that in *Plesiadapis* (Gingerich, in press). Discussion of the relative tooth movements involved in forming each facet have been detailed by Kay and Hiiemäe (1974a) and Gingerich (in press).

Orthal retraction facets have not been detected in carpolestids.

Lower Teeth (Figs. 36, 37). All seven Phase I facets occur on one or more of the molars of each genus. Facets 1 and 5, on the posterior surface of the trigonid, differ markedly in size on the different molars. An oblique ridge (formed by the contact of the cristid oblique with the protocristid)

[1] Precise definitions of these three terms are presented by Kay and Hiiemäe (1974a).

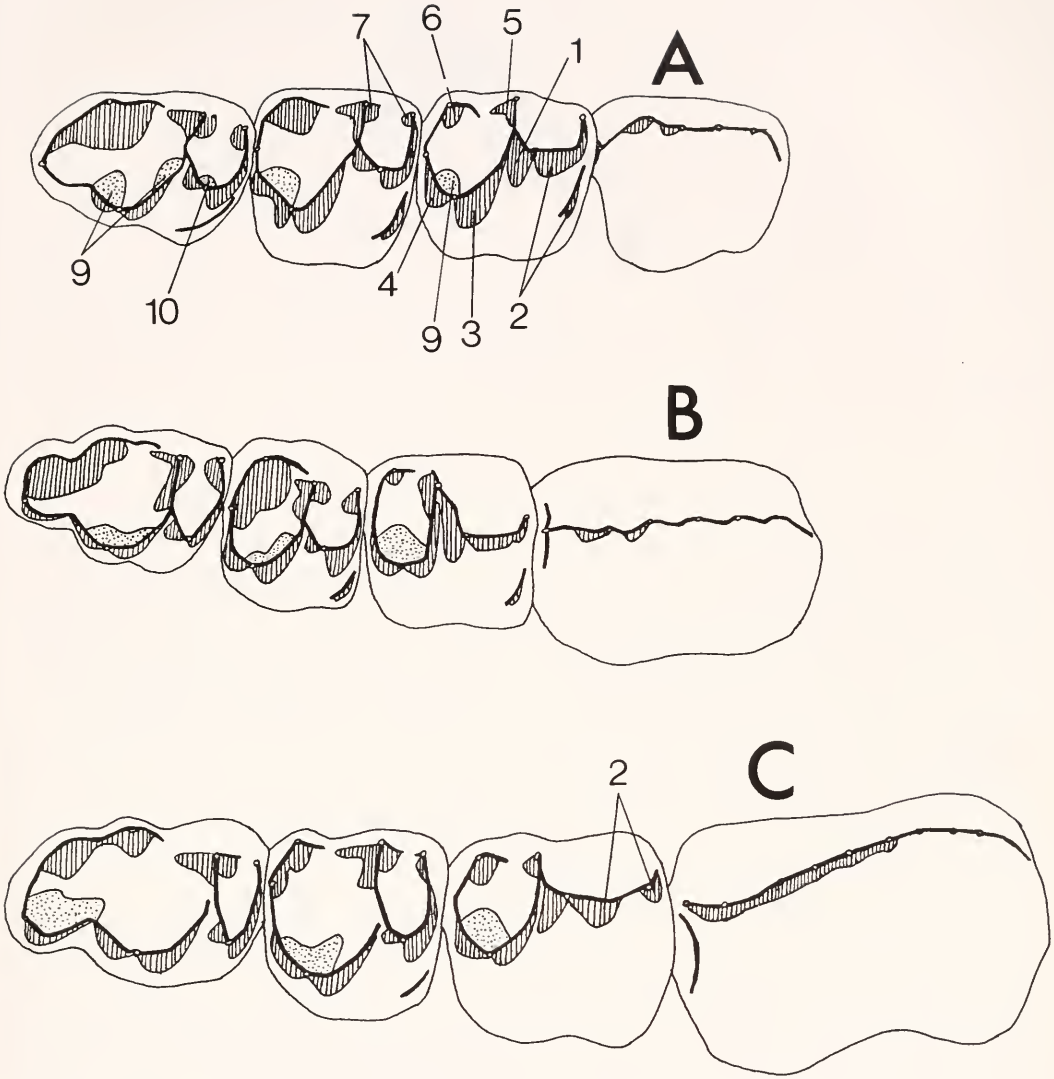


Figure 36. Occlusal wear facets of lower teeth, P_4–M_3. Vertical lines denote Phase I facets; stippling denotes Phase II facets. Numbering of facets is after Crompton (1971) and Kay and Hiiemäe (1974b). A) *Elphidotarsius*; B) *Carpodaptes*; C) *Carpolestes*.

demarcates facet 1, on the posterior surface of the protoconid, from facet 5, on the posterior surface of the metaconid. On M_1, in which the protoconid is the highest cusp, facet 1 is as large as or larger than facet 5, while on M_2 and M_3, where the metaconid is as high or higher than the protoconid, facet 5 is larger than facet 1. The enlargement of facet 5 at the expense of facet 1 appears to be typical of many primates. Facet 2 is lengthened on M_1 by virtue of the elongation of the trigonid. In some specimens an additional shearing surface parallel to facet 2 is developed on the anteroexternal cingulum (M_1 or M_2), as in *Plesiadapis* (Gingerich, in press). Facet 6

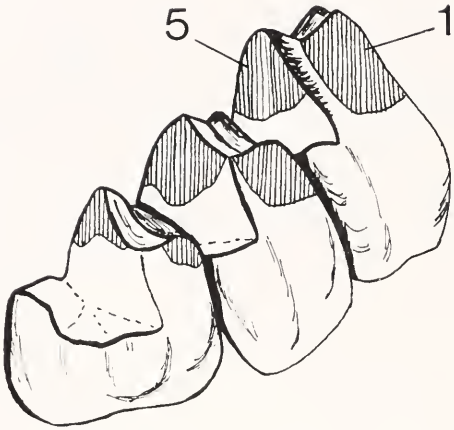


Figure 37. Occlusal wear facets 1 and 5 (Phase I) in *Elphidotarsius* (posterior oblique view of right M_{1-3}).

develops on the buccal surface of the entoconid and may extend to include the hypoconulid region. This facet is most extensive and best developed on M_3. Facet 7, variably developed on the buccal surface of the paraconid and metaconid, is a continuation of facet 6 of the next anterior tooth (Kay and Hiiemäe, 1974a) and in some cases these two facets appear to be confluent with facet 2 (on the paracristid). Shearing surfaces may be increased in number by fenestration of any Phase I facets; this is, of course, prevalent in individuals at advanced stages of wear.

Shearing facets (Phase I) on P_4 are, surprisingly, poorly developed or absent from most specimens. A few specimens of *Elphidotarsius* reveal small striated facets, probably homologous with facets 1 and 5, on the posterobuccal surface of the two posterior apical cusps (the presumed homologues of the protoconid and metaconid). Specimens of *Carpodaptes*, as a rule, show no better-developed wear surfaces than in *Elphidotarsius*. In *Carpolestes* some individuals have small striated facets on the buccal surface of apical cusps on the posterior two-thirds of the tooth. These small facets become confluent on a few heavily-worn individuals (e.g. PU 19030; see Fig. 39D). A few specimens of P_4 in *Carpolestes* display heavy abrasive wear (Fig. 39). No P_4's examined show such extensive Phase I facets as indicated by Butler (1973: fig. 11).

Phase II facets are much less clear than those of Phase I. Facet 9, on the lingual surface of the hypoconid, has been detected on one or more molars of each genus, but facet 10, on the lingual surface of the protoconid, has been observed only on M_3 on a few (e.g. *Elphidotarsius*, PU 14285). This is in accord with Butler's (1973) observation that Phase II facets are best developed on M_3 and less so anteriorly. There are no Phase II facets on P_4, i.e., there is no wear on the lingual side of P_4.

Upper Teeth (Fig. 38). Phase I facets 1–7, matching those of the lower molars, are developed on upper molars of all three genera. As in *Palenochtha* (Kay and Hiiemäe, 1974a) and *Plesiadapis* (Gingerich, in press), facets 1–4 are developed on the conule crests as well as on the preparacrista, centrocrista, and postmetacrista; parallel crests are labelled "a" and "b". For example, facet 1a forms on the preparacrista, 1b on the preparaconule crista, parallel to the preparacrista. Facets 1b, 2b, 3b, and 4b are well developed on M^1 and M^2; hence the conules are large. On M^3 facet 2b is not developed and the metaconule is small. Facet 5, on the lingual surface of the preprotocrista, is prominent on all three

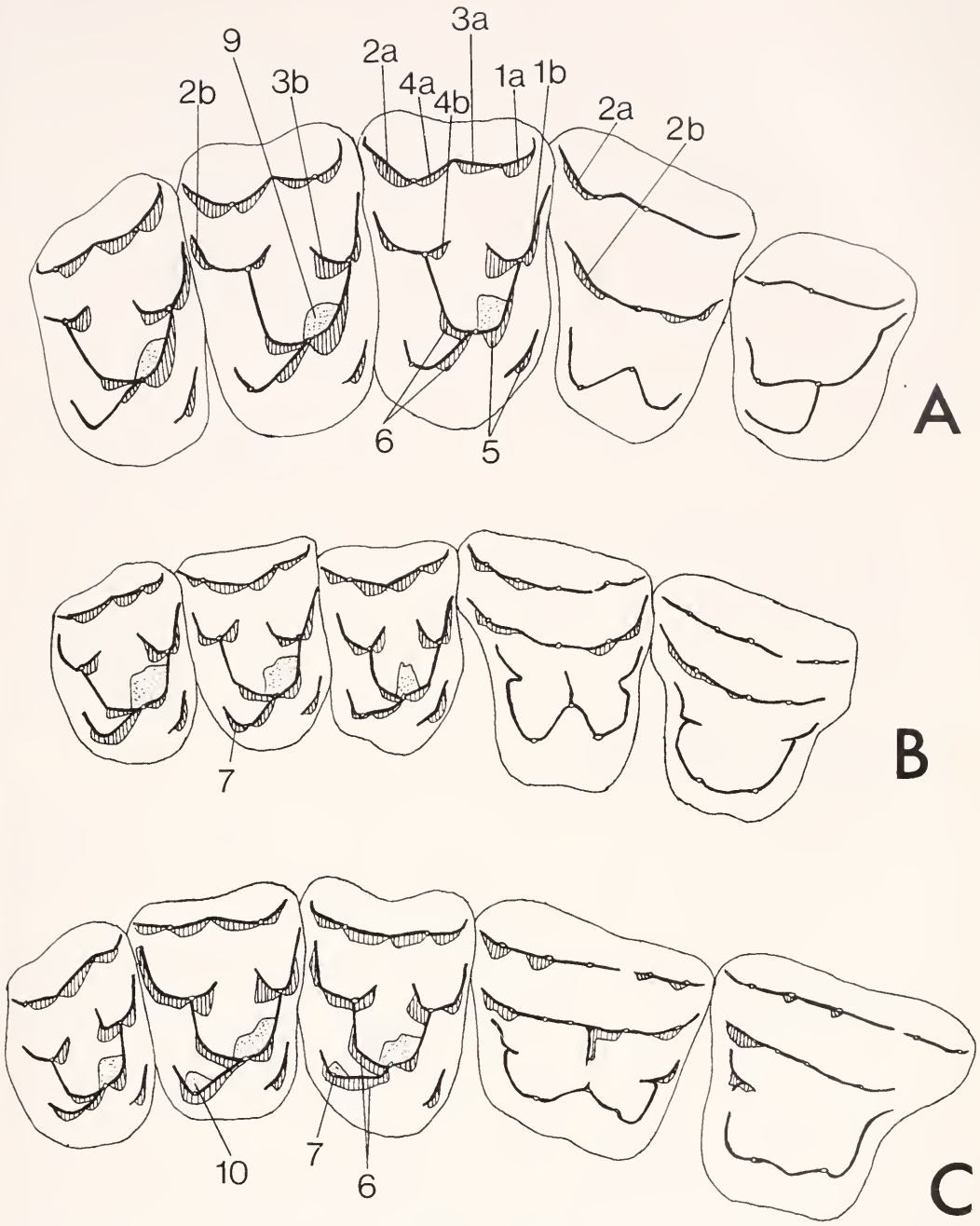


Figure 38. Occlusal wear facets of upper teeth (P^3–M^3), depicted as in Figure 36. A) *Elphidotarsius*; B) *Carpodaptes*; C) *Carpolestes*.

molars and in *Carpodaptes* and *Carpolestes* extends onto the precingulum in many individuals. Facet 6 forms on the postprotocrista and on the "nannopithex fold" (the crest joining the protocone and hypocone). It is confluent with facet 7 on the lingual surface of the hypocone. Facet 7 was not detected in *Elphidotarsius*.

As in the lower molars, Phase II facets are less evident than Phase I facets, but facet 9, on the buccal surface of the protocone, is relatively distinct in many specimens. Facet 10, on the buccal side of the hypocone, was observed only in a few individuals of *Carpolestes*.

P^{3-4} are somewhat difficult to interpret, for although numerous specimens are now available, many show little or no wear. Phase I facets are developed on the lingual surfaces of the posterior third of the buccal and central crests on P^4 in all three genera. These match facet 2 on the trigonid of M_1 and are homologous with facets 2a and 2b on the molars. The significant wear on P^3 and P^4 appears to be due to abrasion, causing the tips of the cusps in the buccal and central crests to become blunt and fenestrated (Figs. 39G, H). This type of wear in *Carpodaptes* and *Carpolestes* is particularly evident on the posterior half of P^3 and anterior half of P^4, i.e., the region which occludes with P_4. Small striated wear facets form on the flattened periphery of these cavitations in some specimens, and in *Carpolestes* they may extend to the short crests between the central and lingual row of cusps. They are not so large as depicted by Butler (1973: fig. 11), indicating that Phase I wear in P^{3-4}, although present, is of minor importance. No phase II facets have been detected on P^3 or P^4 of any carpolestid.

Interpretation. These observations indicate that the molars of carpolestids functioned very much like those of *Plesiadapis*, but Phase II was evidently less prominent than in the latter genus and seems to have been much less important than Phase I. The molars were the significant teeth involved in shearing (Phase I) and grinding (Phase II); the specialized premolars were less effective during this stage of mastication. Shearing capability in the molars was enhanced by increasing the number of shearing surfaces in the same ways as has been observed in *Palenochtha* and *Plesiadapis*. One method, called "en echelon" shear (Hiiemäe and Kay, 1972), involves the development of successive shearing surfaces (e.g., in upper molars, facets 1a and 1b, or facet 5 on both preprotocrista and precingulum; in lower molars, facet 2 on both paracristid and anteroexternal cingulum; see Figs. 36, 38). Individual shearing surfaces were multiplied by fenestration as in *Plesiadapis* (Gingerich, in press). Grinding, the major function in Phase II, involved all the molars but was more prominent posteriorly, as noted also by Butler (1973).

The function of the peculiar, specialized P_4 and P^{3-4} of carpolestids is of particular interest. My conclusions differ somewhat from those of Butler (1973). Despite its bladelike appearance, P_4 was apparently not used primarily in shearing. Phase I facets observed on a few specimens indicate that such function occurred to a limited extent, but the poor development or absence of these facets on the majority of specimens indicates that P_4 was not very important during Phase I. The absence of Phase II facets indicates that P_4 was insignificant in Phase II function.

The premolars of many mammals are involved chiefly in the preparation of food prior to the masticatory stage involving Phase I and II. This "puncture-crushing" stage results in abrasion. P_4 and P^{3-4} of carpolestids display mainly abrasive wear, which has resulted in erosion of the tips of the cusps and exposure of dentine in heavily worn individuals (Fig. 39). The term "puncture-crushing" seems inappropriate to describe the probable use of these teeth in carpolestids, however. P_4 probably functioned in a sawlike manner, cutting or tearing food which was held partly by the polycuspate P^{3-4}. Phase I facets in P^{3-4}, as in P_4, are poorly developed and often absent, suggesting that Phase I shearing was not the primary function of these teeth. Similarly, the absence of Phase II facets on P^{3-4} indicates that their function was insignificant during this stage of mastication.

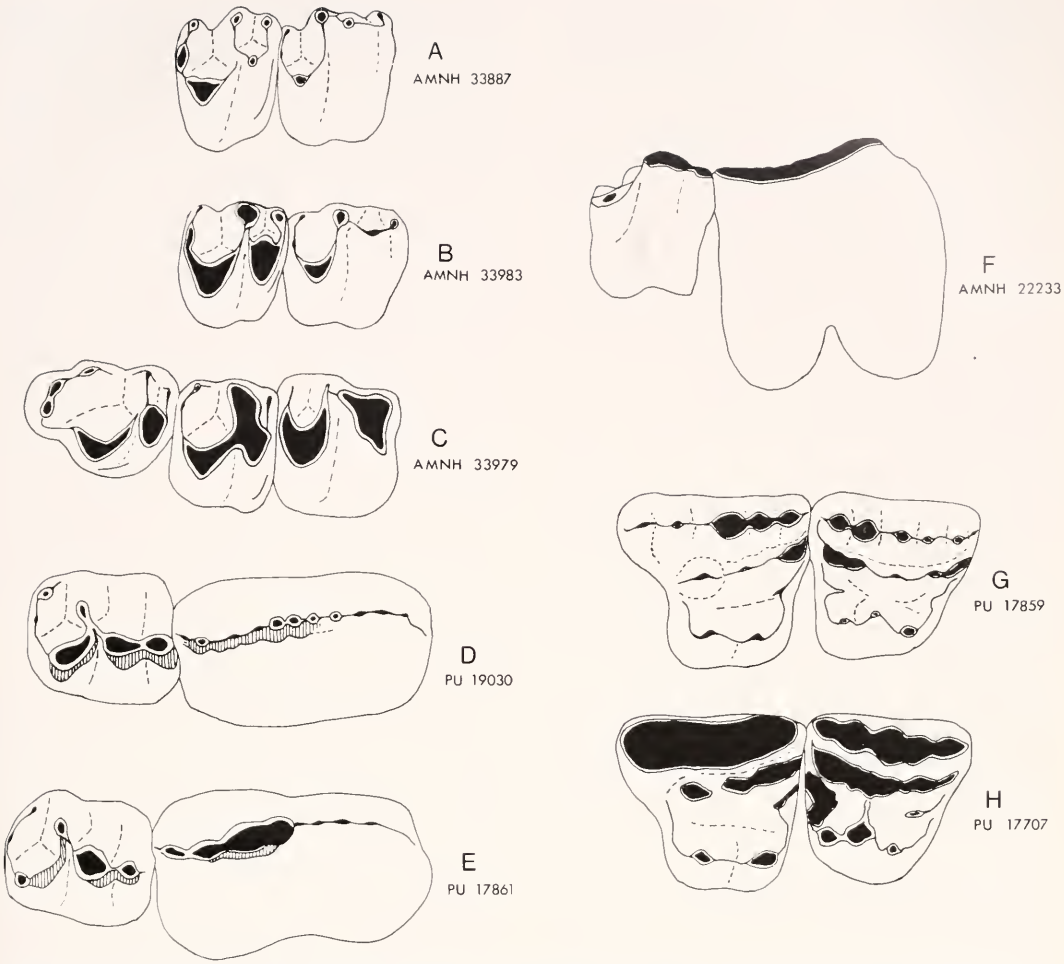


Figure 39. Abrasive wear in carpolestids, exposing dentine (black areas). Vertical lines in D and E are Phase I wear facets. A–C) progressive degrees of wear in *Carpodaptes hazelae*. A and B are right M_{1-2}; C is right M_{1-3} (crown views). D–H) progressive stages of wear in *Carpolestes*. D and E are right P_4–M_1 of *C. dubius* (crown views); F is right P_4–M_1 of *C. nigridens* (lateral view); G and H are left P^{3-4} of *C. dubius* (crown views).

Dietary Inferences

Even in extant mammals it is often difficult, from dental and mandibular structure, to postulate specific feeding preferences. In extinct forms, which often have no living analogues, inferences regarding diet must be largely speculative. Concerning dietary habits of Paleocene mammals in general, Van Valen and Sloan (1966: 264) have remarked:

"Upon considering the diversity of food habits of recent species with teeth generally similar among the species, we are impressed with the impossibility in the foreseeable future of reconstructing in any detail the diets of Paleocene mammals. When there is a phyletic trend towards a more herbivorously adapted dentition, it is probably valid to say that most of the later members of this clade were herbivorous, or more

herbivorous than their ancestors. There are very few Paleocene mammals of any kind for which a more detailed statement on diet is possible."

While specific food preferences of extinct forms may be impossible to establish, some general comments may nevertheless be offered. As noted above, it is probably invalid to base inferences regarding the diet of carpolestids on extant "plagiaulacoid" marsupials. The functional interpretations discussed above show that carpolestids used their molars much as plesiadapids did. Unfortunately, this provides little precise insight, of course, for the diet of plesiadapids can only be speculative. Carpolestid premolars were probably used primarily during the puncture-crushing stage of mastication, suggesting that the diet of carpolestids may have consisted of herbage, fruits, and seeds tougher than those eaten by *Plesiadapis*. Similarities in morphology and wear patterns between carpolestid molars and those of the Recent *Tarsius*, a predominantly insectivorous primate, further suggest that carpolestids were capable of feeding on insects and may have included them in their diet.

ORIGIN, AFFINITIES, AND INTERRELATIONSHIPS OF CARPOLESTIDS

Simpson (1937a: 8) remarked: "In spite of the extraordinary specialization of the premolars, the facts now known about the carpolestid dentition seem to me to point to the early primates and to no other group." I agree totally with this statement. Some early authors (e.g., Matthew and Granger, 1921; Jepsen, 1930), however, did not recognize carpolestids as definite primates, and some recent students have continued to question their primate status. Saban (1961) listed them as Mammalia, *Incertae sedis*. Martin (1968) and Charles-Dominique and Martin (1970) have suggested that allocation of *Plesiadapis* and its allies to the Primates should be reassessed.

Cartmill (1972) recently advocated the more drastic step of transferring the "archaic prosimians" from the Primates to the Insectivora, an unsatisfactory solution which does not accurately reflect the phylogenetic relationships of these forms. Although the evidence now at hand indicates that some archaic prosimians did not possess the three features that Cartmill selected as diagnostic of Eocene and later primates (postorbital bar, petrosal bulla, and opposable hallux or pollex with nail), the dental evidence points overwhelmingly to primate, not insectivoran, affinities, and it is the dentition that constitutes most of the known evidence of the archaic prosimians. Known Paleocene primates are not generally considered ancestral to later ones, and it is only to be expected that they should have remained primitive in some features that later, and perhaps independently, evolved in the primate stock. If one accepts Cartmill's three features as definitive of the Primates, the only recourse would be to establish a new order for the Paleocene forms. In our present state of knowledge, such a move would be premature. I believe that the mainly Paleocene archaic prosimians are definitely primates and should be grouped in the infraorder Plesiadapiformes (Simons, 1972)[1].

It has long been recognized that carpolestids share numerous features with members of the Plesiadapidae, and comparisons of carpolestids with all other Paleocene primates indicate that the closest affinities are with that family. Simpson (1937b: 162) noted the striking likeness of *Elphidotarsius* to *Pronothodectes*. "M_{2-3} are almost exactly like those of *Pronothodectes*, so much so that were this form known from those teeth alone it would have to be defined as a species of *Pronothodectes*." He later wrote (Simpson, 1940: 205): "There is a remarkably close resemblance in the lower molars

[1] The suborder Plesiadapoidea Romer, 1966, is rejected here because it was proposed conditionally, and because it is a homonym of the superfamily Plesiadapoidea Trouessart.

between carpolestids and plesiadapids, but it does not extend to all parts of the dentition and may indicate nothing more than that all are early primates." This now seems to be an overly cautious view. There are, in fact, marked similarities of *Elphidotarsius* to *Pronothodectes* extending beyond the lower molars (see Fig. 41). Upper teeth of *Elphidotarsius,* unknown when Simpson wrote, are even closer structurally to those of *Pronothodectes* than are the lowers. The upper molars are virtually indistinguishable (except in size) from those of *Pronothodectes,* and P^{3-4} are noticeably similar in both genera. I_2, $\overline{C}$, and P_2 are reduced in both forms, and the dental formulae are the same as far as can be determined. These resemblances, and the lack of such close similarity to other archaic primates, argue strongly for community of origin of the two families (as Simpson [1937a] suggested), probably in the Puercan.

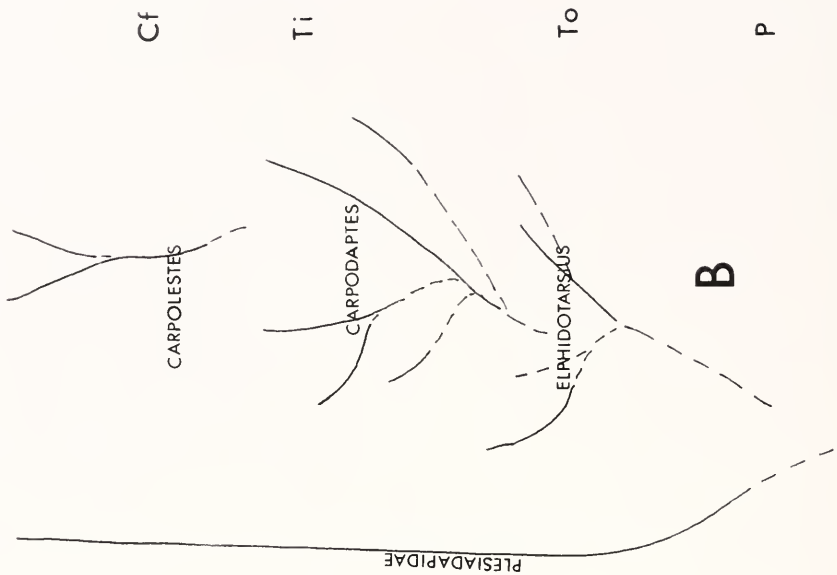
Van Valen (1969: 295) proposed that carpolestids evolved "from *Pronothodectes* or just possibly some unknown more primitive plesiadapid." The latter alternative seems more probable, inasmuch as *Pronothodectes* is not known from strata below those which contain *Elphidotarsius.* A new, undescribed, plesiadapoid genus from Purgatory Hill (Sloan, 1969) may shed light on this problem. As demonstrated above, derivation of *Elphidotarsius* from a *Pronothodectes*-like form would not be difficult. Virtually no modification of the molars would be involved, the trigonid of M_1 being only slightly extended in *Elphidotarsius.* P_4 of *Elphidotarsius* may be termed submolariform, the apical cusps homologous to the three trigonid cusps (with the addition of an anterior accessory cuspule), and a talonid cusp behind. P_4 is typically premolariform in *Pronothodectes.* In the Puercan *Purgatorius unio,* it has a distinct paraconid and may show enamel thickenings in the metaconid region (Clemens, 1974). Of the upper premolars, P^4 has three longitudinal crests in both *Elphidotarsius* and *Pronothodectes.* P^3 in the former, however, is not divided into three longitudinal parts, as in *Pronothodectes* (and later carpolestids). The simpler P^3, like that of *Elphidotarsius,* was probably the ancestral condition. Carpolestids and plesiadapids should be placed in a superfamily Plesiadapoidea (along with *Saxonella*), to reflect their close relationship.

Intergeneric relationships of carpolestids are easily interpreted. The conclusion reached here is that the three genera are members of a single lineage. All three are found in the same general area and they constitute a morphologic sequence found in successive strata. It is highly probable that *Elphidotarsius* gave rise to *Carpodaptes,* and the latter gave rise to *Carpolestes* (Fig. 40B). No known evidence contradicts this hypothesis.

Some authors (e.g. Schaeffer et al., 1972) advocate a much more complex interpretation of phylogeny, suggesting that taxa that seem to form a direct lineage with regard to morphology and stratigraphy may actually represent only a few members of a much wider radiation. The application of this concept to carpolestid phylogeny might lead to the conclusion that the three genera do not lie in a single lineage (Fig. 40A).

For example, the sympatric occurrence of *Carpodaptes* and *Elphidotarsius* in the Late Torrejonian Shotgun Local Fauna may suggest that there were two carpolestid lineages, one involving only *Elphidotarsius,* the other comprised of *Carpodaptes* and *Carpolestes.* However, *Elphidotarsius* is known also from Torrejonian beds almost surely older than those at Shotgun, which is the earliest occurrence of *Carpodaptes.* The antecedents of *Carpodaptes* must have passed through a stage, structurally like *Elphidotarsius,* that would be considered in that genus as now defined. No features of *Elphidotarsius* now known exclude it from a position ancestral to *Carpodaptes.*

Even closer resemblances between *Carpodaptes* and *Carpolestes* indicate that these genera must lie in an ancestor-descendant line. Simpson (1937b) was of the



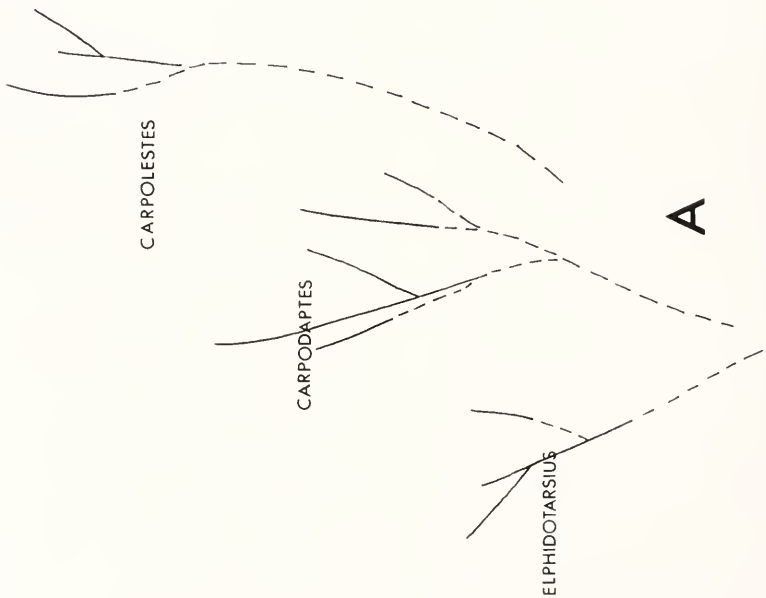


Figure 40. Possible phylogenies of the Carpolestidae (see text).

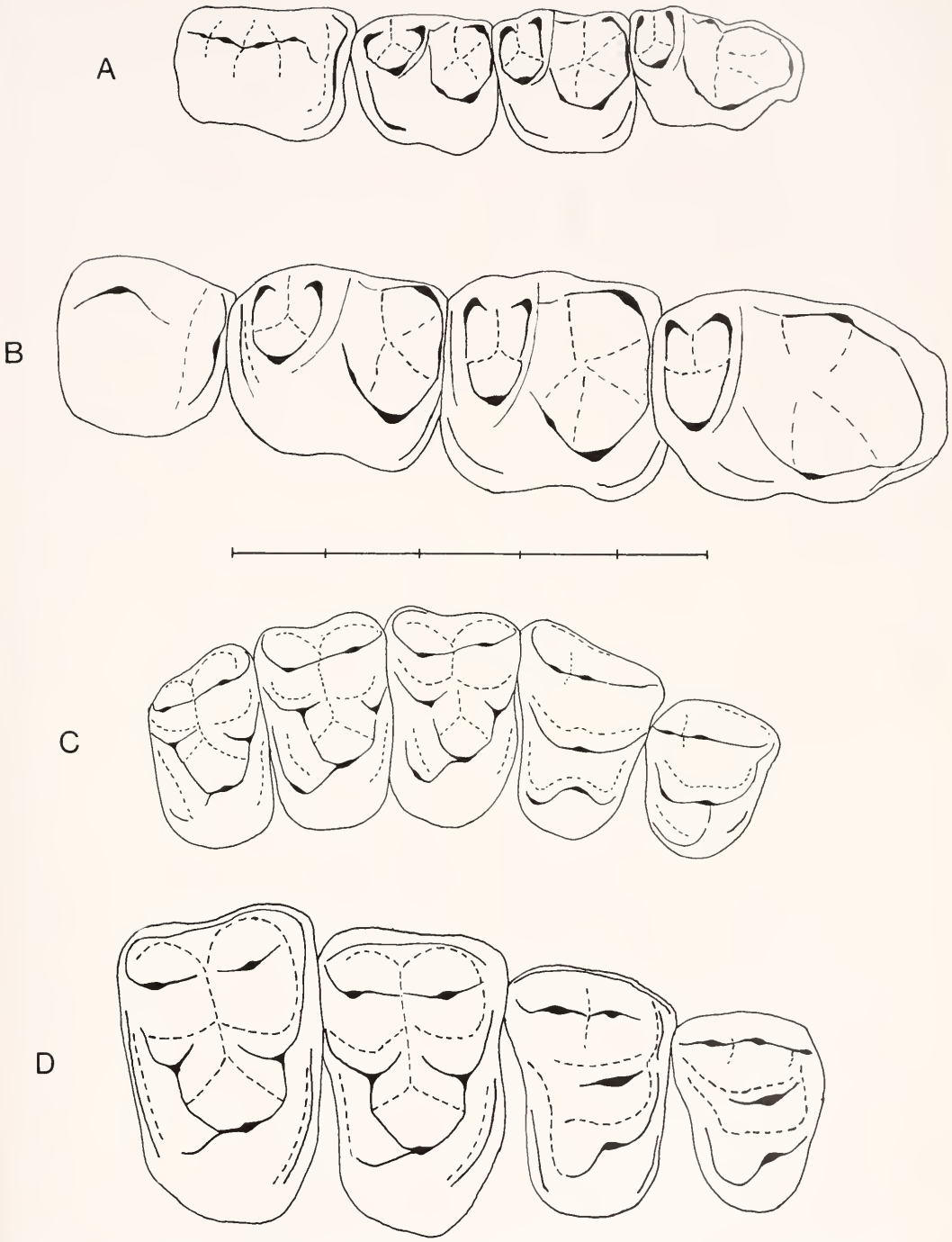


Figure 41. Comparison of *Elphidotarsius* with *Pronothodectes*, to same scale (mm). A) *Elphidotarsius* sp., cf. *E. florencae* Gidley, PU 14282, left P_4–M_3. B) *Pronothodectes matthewi* Gidley, AMNH 35462, left P_4–M_3. C) *Elphidotarsius* sp., cf. *E. florencae* Gidley, PU 17439, right P_3–M_3. D) *Pronothodectes matthewi* Gidley, AMNH 35470, left P^3–M^2 (reversed).

opinion that these two had evolved in parallel, for he did not believe the age difference between them to be significant. As they are now known, however, all specimens of *Carpodaptes* are invariably from lower strata than those of *Carpolestes*, so Simpson's objection is no longer tenable.

Relationships among carpolestid species are more nebulous. Limited geographic occurrences of most species and our ignorance of precise stratigraphic correlations between many sites make relative age determinations difficult for some species, particularly of the genus *Carpodaptes*. I shall not propose a detailed reconstruction of carpolestid phylogeny, therefore, but some comments may be offered.

Of the two species of *Elphidotarsius*, *E. florencae* is structurally more primitive. *E. shotgunensis* has a longer P_4 and more extended M_1 trigonid, features which place it closer structurally to *Carpodaptes*. However, it is known only as a Late Torrejonian contemporary of *Carpodaptes*, at Shotgun, and unless present at an earlier time, it must be eliminated from consideration as a *Carpodaptes* ancestor.

Relationships among the species of *Carpodaptes* are poorly known. The morphology of *C. aulacodon* provides no immediate clue to its relationships with other species of the genus. The shape of P_4 and configuration and definition of the apical cusps indicate no particularly close relationship to any other species of the genus, nor special proximity to the ancestry of *Carpolestes*.

Carpodaptes hazelae, although the best represented species of the genus, is also difficult to place phylogenetically. Features such as the often well defined apical cusps and the separated talonid cusps of P_4 suggest that this species is not particularly close to the direct ancestry of *Carpolestes*. On the other hand, P^{3-4} are quite similar to those of *Carpolestes*. (It must be emphasized that upper teeth are known in only one other species of *Carpodaptes*.)

Carpodaptes cygneus and *C. hobackensis* are very closely allied species or, just possibly, variants of the same species. Morphologically, they possess certain features definitely foreshadowing those present in *Carpolestes*: usually poorly defined apical cusps on P_4, talonid of P_4 not so clearly separated from the P_4 blade, S-shaped conformation of P_4 cusps in crown view, and posterolingual depression in P_4 (*C. hobackensis*). These features led Dorr (1952) to conclude that *C. hobackensis* was probably nearer the direct line of ancestry to *Carpolestes* than either of the other species of *Carpodaptes* then known (*C. aulacodon* and *C. hazelae*). Although this is possible, it must be noted that *C. hobackensis* and *C. cygneus* are the smallest known species of *Carpodaptes* and are, in fact, even smaller than the known species of *Elphidotarsius* in molar dimensions. This may indicate that their particular line of evolution trended toward smaller size, possibly posing an obstacle to their lying in direct ancestry to *Carpolestes*. A hypothetical larger form with morphology like that of *C. hobackensis* would be an ideal ancestor for *Carpolestes*.

Among known species, *Carpodaptes jepseni* appears to be nearest to the ancestry of *Carpolestes*. In support of this conclusion are the large size, shape of P_4, and the size of P_4 relative to the molars. The presence of only six relatively well defined apical cusps and a distinct talonid cusp on P_4 are features typical of *Carpodaptes*. If this species is not in or near the ancestry of *Carpolestes*, it must represent a line which closely approached the *Carpolestes* grade of specialization. As with *C. aulacodon*, caution must be exercised in drawing conclusions based on a single specimen.

The two recognized species of *Carpolestes* are unquestionably very closely related. The slightly more specialized P^3 of *C. nigridens* indicates that this species was a direct derivative of *C. dubius*. This is the only differentiating character discernible in known specimens. Alternatively, the

two may have been representatives of a single polytypic species, but this cannot be substantiated on the basis of present evidence.

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APPENDIX

Table I. Dimensions of mandibular teeth of carpolestids (mm).

Spec. No.	P_4L	P_4B	M_1L	M_1B	M_2L	M_2B	M_3L	M_3B	MD
Elphidotarsius florencae Gidley, holotype									
USNM 9411	1.7	1.3	1.3	1.2	1.3	1.3	1.8	1.1	3.1
Elphidotarsius sp., cf. *E. florencae* Gidley, from Rock Bench Quarry									
PU 14282	1.8	1.6	1.5	1.5	1.5	1.6	2.0	1.4	3.1
PU 14283	1.7	1.3	1.5	1.5			2.0	1.2	3.0
PU 14284	1.7	1.3	c.1.5		1.4	1.4			3.0
PU 14285	1.8	1.5	1.5	1.4	1.4	1.5	1.9	1.3	3.1
PU 14286	1.9	1.5			1.4	1.6	1.9	1.4	c.3.1
PU 14791	1.7	1.3	1.5	1.3	1.4	1.4	2.0	1.3	2.9
PU 14792	1.7	1.4	1.5	1.3	1.5	1.4	1.8	1.2	2.8
PU 14794			1.5	1.5	1.3	1.5	2.1	1.3	3.3
PU 14795					1.4	1.6	c.2.0		
PU 14796	1.9	1.5	1.5	1.4					
PU 14843			1.4	1.4	1.3	1.5	1.9	1.3	
PU 17742	c.1.9		1.5	1.5	1.3	1.4			3.4
PU 18462	1.8	1.3							
PU 18463			1.5	1.4	1.4	c.1.5			
PU 18671	1.8	1.4					1.9	1.3	c.3.0
PU 18675	1.8	1.5	1.5	1.5	1.5	1.5			3.2
PU 19801			1.6	1.6	1.6	1.7			3.3
PU 21546	1.9	1.3	1.5	1.3	1.4	1.4	1.9	1.2	3.0
PU 21547	1.9	1.5	1.5	1.5	1.4	1.5			3.5
PU 21550	1.7	1.3							
PU 21551	1.7	1.3							

TABLE I [CONTINUED]

Spec. No.	P_4L	P_4B	M_1L	M_1B	M_2L	M_2B	M_3L	M_3B	MD
Elphidotarsius sp., cf. *E. florencae* Gidley, from Medicine Rocks site 1									
PU 16916		c.1.3	1.5	1.3	1.5	1.3			2.7
PU 19764	1.6	1.3	1.4	1.4	1.4	1.4			3.0
PU 19780		c.1.2	1.4	1.3					
Elphidotarsius shotgunensis Gazin									
AMNH 88311	2.0	1.2	1.4	1.1					
MCZ 18775			1.6	1.3					
Carpodaptes aulacodon Matthew and Granger, holotype									
AMNH 17367	2.7	1.7	1.5	1.5	1.3	1.5	1.7	1.2	3.3
Carpodaptes hazelae Simpson, from Scarritt Quarry									
AMNH 33853	2.6	1.7	1.6	1.4	1.3	1.5			c.3.7
AMNH 33854	2.5	1.7	1.5	1.5	1.2	1.4	1.9	1.2	3.8
AMNH 33887	2.6	1.7	1.5	1.4	1.4	1.4			3.8
AMNH 33979			1.5	1.6	1.4	1.6	1.9	1.4	
AMNH 33980	2.6	1.7	1.5	1.5	1.5	1.5	2.0	1.3	3.7
AMNH 33983			1.6	1.5	1.3	1.4			
AMNH 33984			1.4	1.4	1.3	1.5	1.8	1.2	
Carpodaptes hazelae Simpson, from Cedar Point Quarry									
PU 19558	2.4	1.7	1.4	1.3					
PU 19572	2.5	1.5	1.4	1.4					3.5
PU 19574	2.2	1.3	1.5	1.3	1.3	1.3	1.8	1.1	c.3.1
PU 19596	2.4	1.5	1.5	1.5					3.3
PU 19601	2.6	1.5							
PU 19936			1.5	1.4	1.3	1.5			3.4
PU 19953	2.7	1.8	1.4	1.3					
PU 19954	2.5	1.5							
PU 19955	2.5	1.8	1.5	1.2	1.2	1.3			3.3
PU 19958	2.4	1.6	1.5	1.3	1.2	1.4	1.8	1.1	
PU 19968	2.8	1.7	1.5	1.4					3.5
PU 19969	2.5	1.4							
PU 19985	2.4	1.4							
PU 20007	2.4	1.3	c.1.4	1.3					
PU 20010	2.4	1.5	1.5	1.3					
PU 20011	2.5	1.6			1.3	1.3			3.4
PU 20034			1.6	1.4					
PU 20060	2.2	1.4	1.3	1.2	1.1	1.3			3.1
PU 20064	2.4	1.4	1.3	1.3	1.2	1.3			3.5
PU 20068	2.5	1.5	1.5	1.3	1.3	1.3			3.5
PU 20084	2.6	1.6	1.5	1.4	1.3	1.4	2.0	1.3	3.6
PU 20087	2.5	1.6	1.4	1.3	1.3	1.4			3.3
PU 20610	2.5	1.6	1.5	1.4	1.4	1.4			3.5
PU 20615	2.4	1.4	1.5	1.3					3.3
PU 20630	2.3	1.4	c.1.3	c.1.2	1.2	1.2	1.7	1.0	3.2
PU 20634	2.6	1.6	1.5	1.2					
PU 20656	2.3	1.4	1.6	1.4	1.4	1.3			3.3
PU 20719	2.4	1.6	1.3	1.3	1.3	1.3	1.9	1.1	3.3
PU 20808	2.6	1.5	1.6	1.5					c.4.0
PU 20812	2.3	1.6	1.4	1.3	c.1.2	1.3			3.5
PU 20820	2.5	1.5	1.5	1.3	1.3	1.3			3.3
PU 20839	2.5	1.8	1.5	1.4	1.3	1.4	1.9	1.3	3.6

Table I [continued]

Spec. No.	P_4L	P_4B	M_1L	M_1B	M_2L	M_2B	M_3L	M_3B	MD
PU 20840	2.1	c.1.2							
PU 20886	2.3	1.6	1.4	1.3					
PU 20889	2.7	1.8	1.5	1.5	1.4	1.5			3.8
PU 20898	2.7	1.7	1.4	1.4					3.7
PU 20900	c.2.4		1.5	1.3	c.1.3	c.1.3			
PU 21213	2.4	1.5	1.5	1.3	1.2	1.3	1.9	1.1	3.4
PU 21266	2.3	1.5							
PU 21279	2.4	1.5	1.5	1.3	1.3	1.4			
PU 21297	2.6	1.5	1.5	1.4	1.3	1.4			3.8
PU 21299	2.5	1.6	1.4	1.3	1.3	1.3			3.4
PU 21316	2.5	1.6	1.4	1.4					3.9
PU 21317	2.4	1.5	1.5	1.3	1.3	1.4			
PU 21330	2.4	1.5	1.5	1.3	1.3	1.3			
PU 21341	2.4	1.6	1.5	1.3	1.3	1.4	2.0	1.2	3.4
PU 21350	2.4	1.5	1.4	1.2	1.3	1.3	1.8	1.2	3.3
PU 21351	2.4	1.4	1.4	1.2	1.2	1.2	1.7	1.1	
PU 21357			1.6	1.5	1.4	1.5	c.2.0	c.1.3	
PU 21384	2.7	1.5	1.4	1.3	1.3	1.4	1.9	1.2	3.8
PU 21393	2.5	1.5							
PU 21399	2.5	1.5	1.5	1.2	1.3	1.3	1.9	1.1	3.5
PU 21413	2.6	1.6	1.5	1.2	1.4	1.2	1.8	1.1	3.5
PU 21419	2.4	1.4	1.5	1.2					3.2
PU 21437	2.7	1.6							
PU 21438	2.2	1.3			1.3	1.3			
Carpodaptes hobackensis Dorr									
UMMP 27233	2.2	1.2	1.4	1.2	1.4	1.2			
UMMP 27234	2.3	c.1.2	1.3	1.2					
UMMP 27253	c.2.3	1.3							
UMMP 55124	2.2	1.2	1.5	1.2	1.3	1.3	1.8	1.1	
Carpodaptes cygneus Russell, from Swan Hills									
ROM 5622	2.2	1.2							
ROM 5623	2.0	1.2							
Carpodaptes sp., cf. *C. cygneus* Russell, from Cypress Hills, Alberta									
UA 5874	2.3	1.5							
UA 5875	2.1	1.4							
UA 5876	2.2	1.5							
UA 5877			1.5	1.5					
UA 5878					1.5	1.4			
UA 5879					1.4	1.4			
UA 5880							1.8	1.1	
UA 5881							1.8	1.1	
Carpodaptes jepseni, new species, holotype									
PU 20716	3.2	2.2	1.9	1.7	1.7	1.7			c.5.5
Carpolestes nigridens Simpson, from Bear Creek									
AMNH 22159	3.3	1.9	1.9	1.6	1.6	1.6			5.1
AMNH 22187	3.1	1.8							
AMNH 22188	3.1	2.0							
AMNH 22190	2.9	1.7	1.8	1.4	1.5	1.3			5.0
AMNH 22233	3.0	1.9	1.8	1.5	1.6	1.5	2.3	1.4	5.0
PU 20718	3.0	2.1	1.8	1.6					5.0
CM 11518			1.8	1.6					
CM 11524	3.3	1.9							

TABLE I [CONTINUED]

Spec. No.	P_4L	P_4B	M_1L	M_1B	M_2L	M_2B	M_3L	M_3B	MD
CM 11549	3.4	1.9							
CM 11557			1.8	1.4					
CM 11665	3.2	1.8							
CM 11702	3.3	1.9							
Carpolestes dubius Jepsen, from Princeton Quarry level									
PU 13275	3.3	2.0	1.9	1.8	1.6	1.6	2.2	1.4	
PU 13276	3.6	2.0	c.1.9	c.1.7	c.1.5	c.1.6			
PU 14235			1.9	1.8	1.5	1.6			
PU 14341			2.0	1.7	1.6	1.5			
PU 14342	3.4	2.1	1.9	1.6					
PU 14344	3.0	2.1	1.8	1.6	1.6	1.6			4.6
PU 14345	3.2	2.0	1.7	1.5					
PU 14346	3.3	1.8	1.9	1.5	1.5	1.4			
PU 17646			1.8	1.5	1.4	1.5	2.3	1.4	4.0
PU 17647			1.6	1.6	1.5	1.5			
PU 17710	c.3.2	c.1.9	1.8	1.5	1.5	1.5	2.0	1.3	4.9
PU 17856			1.8	1.5					
PU 17857	3.3	2.0							
PU 17858	c.3.6	c.2.2	2.0	2.1					
PU 17860	3.6	2.0							
PU 17861	3.5	2.1	1.9	1.8					c.5.0
PU 17926	3.1	2.1	2.0	1.7	1.7	1.7			4.8
PU 19013	3.1	1.8							
PU 19018			1.9	1.6	1.6	1.6			
PU 19023	3.3	2.1							
PU 19030	3.3	1.9	2.0	1.7					
PU 19031	3.2	2.3	1.9	1.6	1.5	1.6			
PU 19064		c.2.1	1.9	1.9					
PU 19095	3.6	2.0							
PU 19109	3.3	2.0							
PU 19385	3.4	2.1	1.9	1.7	1.6	1.6	2.2	1.4	5.3
PU 19406	3.0	2.0	1.7	1.6	1.5	1.5	2.0	1.4	
PU 19409	3.5	2.2	2.0	1.8	1.5	1.6	2.1	1.4	5.5
PU 19849	3.5	2.2							
PU 19886	3.3	1.9	1.9	1.6					
PU 21548	3.3	1.9							
PU 21549	3.3	1.9							
Carpolestes sp., from various localities									
PU 13284	3.0	1.7							
PU 14853	3.5	2.2	1.7	1.5					
PU 18102	3.1	c.1.7							
PU 18315	3.8	2.5	2.0	1.8					
PU 20720			1.8	1.5					
PU 20721	3.2	1.8	1.9	1.5					
PU 21227a	3.1	1.6							
PU 21227b	3.2	2.0	1.9	1.6					
PU 21227c	3.1	2.1	1.8	1.6					
AMNH 88198	3.3	1.9	1.8	1.5	1.5	1.4			5.0
USNM 21280	2.7	1.7							

TABLE II. DIMENSIONS OF MAXILLARY TEETH OF CARPOLESTIDS (MM).

Spec. No.	P^3L	P^3B	P^4L	P^4B	M^1L	M^1B	M^2L	M^2B	M^3L	M^3B
Elphidotarsius sp., cf. *E. florencae* Gidley, from Rock Bench Quarry										
PU 17439	1.3	1.6	1.6	2.1	1.4	2.2	1.3	2.2	1.2	2.0
PU 17736			1.5	1.9	1.3	2.1				
Carpodaptes hazelae Simpson, from Scarritt Quarry										
AMNH 33855	2.0	2.2	1.8	2.3						
AMNH 33980	2.0	2.3	2.0	2.6	1.4	2.3	1.4	2.2	1.3	2.0
AMNH 33981	1.9	2.1	1.8	2.3						
AMNH 33982	1.8	2.0	1.5	2.1	1.3	2.1				
AMNH 33985	1.9	2.1								
Carpodaptes hazelae Simpson, from Cedar Point Quarry										
PU 19939	1.9	2.0	1.7	2.2	1.3	1.8	1.2	1.8	1.2	1.6
PU 20065	1.8	2.0	1.7	2.2						
Carpodaptes cygneus Russell, from Swan Hills										
ROM 05624	1.6	1.6								
Carpodaptes sp., cf. *C. cygneus* Russell, from Cypress Hills, Alberta										
UA 5857	1.7	1.8								
UA 5858	1.8	1.8								
UA 5861			1.7	2.1						
UA 5862 [M^2?]							1.3	2.0		
UA 5872									1.1	1.7
Carpodaptes sp., from Princeton Locality 11 in the Crazy Mountain Field										
PU 14639			1.7	2.4	1.4	2.1	1.3	2.0		
Carpoleptes nigridens Simpson, from various localities										
AMNH 22196	3.2	2.4								
PU 17978	3.1	2.3								
PU 19543	2.8	2.3								
YPM 24614	3.3	2.5								
Carpolestes dubius Jepsen, from Princeton Quarry Level										
PU 13305	2.5	2.5	2.2	2.2	1.6	2.1	1.5	2.1		
PU 14069	2.4	2.2	2.1	2.2	1.6	2.2				
PU 14077	2.4	2.3	2.2	2.0	1.5	2.2	1.5	2.0	1.3	1.9
PU 14343	2.5	2.5	2.3	c.2.5						
PU 14347	2.6	2.5								
PU 17707	2.4	2.3	2.1	2.1						
PU 17708							1.5	2.3	1.4	2.2
PU 17709 r	2.5	2.3	2.2	2.2	1.5	2.4	1.5	2.3	1.3	2.0
PU 17709 l	2.4	2.3	2.2	2.2	1.5	2.5	1.5	2.3	1.3	2.0
PU 17859	2.4	2.4	2.2	2.1						
PU 17927	2.6	2.3	2.2	2.2	1.6	2.1				
PU 17963			2.0	1.9	1.5	2.1	1.4	2.0		
PU 19081	2.5	2.4								
PU 19349	2.5	2.7	2.3	2.3	1.8	2.4	1.5	2.3	1.3	2.0
PU 19422 r	2.7	2.5	2.3	2.2						
PU 19422 l	2.7	2.5			1.6	2.4	1.5	2.2	c.1.3	2.0
PU 19436			2.4	2.1						

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SYSTEMATICS AND DISTRIBUTION OF CERATIOID ANGLERFISHES OF THE GENUS *CHAENOPHRYNE* (FAMILY ONEIRODIDAE)

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ABSTRACT. The ceratioid anglerfish genus *Chaenophryne* of the family Oneirodidae is revised on the basis of all known material. Of the 18 available names, four are recognized as species. The five nominal forms, *Chaenophryne longiceps*, *C. crossota*, *C. bicornis*, *C. quadrifilis*, and *C. crenata*, previously forming the *C. longiceps*-group, and *C. haplactis* of the *C. draco*-group, are considered synonyms, taking the oldest available name, *C. longiceps*. The *C. longiceps*-group, now being monotypic, is not recognized. The *C. draco*-group, however, is retained to include larvae and males easily distinguished from those of *C. longiceps* but not divisible into smaller taxonomic units. Included in the *C. draco*-group are three species based on metamorphosed females: *C. draco*, *C. melanorhabdus*, and *C. ramifera*. *Chaenophryne parviconus*, *C. atriconus*, *C. columnifera*, *C. macractis*, and *C. melanodactylus* are considered synonyms of *C. draco*. *Chaenophryne melanorhabdus* with its junior synonym, *C. pterolophus*, is resurrected from synonymy and given specific status. *Chaenophryne pacis* is a synonym of *C. ramifera*. The tentative distribution of each species is plotted, evolutionary relationships are discussed, and a key to the species of the genus is provided.

INTRODUCTION

The genus *Chaenophryne* includes globose, bathypelagic anglerfishes, easily separated from members of allied genera by the absence of sphenotic spines, an operculum that is only slightly concave posteriorly, and peculiar, highly cancellous bones (Bertelsen, 1951:109; Pietsch, 1974a). Regan (1925) established the genus *Chaenophryne* with the description of *C. longiceps* based on 14 specimens, only one of which actually represented the type species. The remaining 13 specimens were included in descriptions of 13 new species introduced by Regan and Trewavas (1932): *C. bicornis*, *C. crenata*, *C. quadrifilis*, *C. haplactis*, *C. parviconus*, *C. atriconus*, *C. columnifera*, *C. melanodactylus*, *C. macractis*, *C. melanorhabdus*, *C. pterolophus*, *C. fimbriata*, and *C. ramifera*. Prior to Bertelsen's (1951) monograph on the Ceratioidei, four additional forms were described: *C. crossota* Beebe, 1932; *C. draco* Beebe, 1932; *C. intermedia* Belloc, 1938; and *C. pacis* Koefoed, 1944. The total number of nominal species is thus 18, 14 of which were based on one or two adolescent female specimens less than 20 mm standard length, none on more than nine specimens, and only one represented by a specimen larger than 24 mm standard length.

From an examination of the extensive larval material in the DANA Collections, Bertelsen (1951) was able to divide the then known material of *Chaenophryne* into two species-groups based on the inner pigment layer and number of pectoral fin-rays. Within the *C. longiceps*-group he tentatively recognized five species: *C. longiceps*, *C. quadrifilis*, *C. bicornis*, *C. crenata*, and *C. crossota*; within the *C. draco*-group three species: *C. draco*, *C. parviconus*, and

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TABLE 1. REALLOCATION OF NOMINAL FORMS OF *CHAENOPHRYNE*.

longiceps-group of Bertelsen, 1951	*longiceps* Regan, 1925	*longiceps* Regan, 1925
	crossotus Beebe, 1932	
	bicornis Regan and Trewavas, 1932	
	crenata Regan and Trewavas, 1932	
	quadrifilis Regan and Trewavas, 1932	
draco-group of Bertelsen, 1951	*haplactis* Regan and Trewavas, 1932	*draco* Beebe, 1932
	draco Beebe, 1932	
	parviconus Regan and Trewavas, 1932	
	atriconus Regan and Trewavas, 1932	
	columnifera Regan and Trewavas, 1932	
	melanodactylus Regan and Trewavas, 1932	
	macractis Regan and Trewavas, 1932	
	melanorhabdus Regan and Trewavas, 1932	*melanorhabdus* Regan and Trewavas, 1932
	pterolophus Regan and Trewavas, 1932	
	ramifera Regan and Trewavas, 1932	*ramifera* Regan and Trewavas, 1932
	fimbriata Regan and Trewavas,1932	
	intermedia Belloc, 1938	
	pacis Koefoed, 1944	

C. ramifera. Chaenophryne fimbriata and *C. intermedia* were considered synonyms of *C. ramifera* and all remaining available names were placed in the synonymy of *C. parviconus.*

In the present paper it is shown that the available female material of *Chaenophryne* represents four well-defined species (Table 1): *C. longiceps*, represented by 33 specimens, collected from all three major oceans of the world; *C. draco,* represented by 46 specimens, also of world-wide distribution; *C. melanorhabdus*, 23 specimens, apparently restricted to the continental slope of western North America; and *C. ramifera*, 15 specimens of world-wide distribution. The separation of these species is based almost entirely on the morphology of the esca. Significant differences exist, however, in the width of the escal bulb, the length of the illicium, jaw tooth counts, and fin-ray counts.

Despite a greater than four-fold increase in material since Bertelsen's (1951) revision, males can be separated into only two taxonomic units corresponding to *C. longiceps* and the *C. draco*-group.

METHODS AND MATERIALS

Standard lengths (SL) were used throughout. Measurements were taken on the left side whenever possible and rounded to the nearest 0.1 mm. To insure accurate fin-ray counts, skin was removed from the pectoral fins and incisions were made to reveal the rays of the dorsal and anal fins. Illicium length is the distance from the articulation of the pterygiophore of the illicium and the illicial bone to the dorsal surface of the escal bulb, excluding escal appendages. Terminology used in describing the various parts of the angling apparatus follows Bradbury (1967). Definitions of terms used for the different stages of development follow those of Bertelsen (1951:10–11). Complete locality data for primary type material is entered in the synonymies. Drawings were made with the aid of a Wild M-5 Camera Lucida.

Since nearly all the available collections of *Chaenophryne* were made with non-closing nets, the actual depth of capture is unknown. For those species represented by sufficient material, vertical distributions were analyzed by a procedure similar to that used by William H. Krueger (unpublished manuscript) for determining depths of capture of *Idiacanthus*, and outlined by Gibbs (1969; see also Pietsch, 1974a). Station data were taken from Schmidt (1929), Carlsberg Foundation (1934), and unpublished data for VELERO

IV cruises of the University of Southern California. For each trawl, the number of hours at depth was multiplied by the area of the mouth of the net. The number of meter-hours for each depth interval, and the number of specimens caught at each depth interval were tabulated and expressed as a percentage of total for comparison. When the percentage of specimens caught at any depth is considerably greater than the percentage of meter-hours at that depth, it may be assumed that this represents a region of concentration. The reverse indicates that specimens recorded for that depth probably were caught while the net was being lowered or raised.

Material used for the comparative osteological investigation was cleared and stained with alizarin red S following the trypsin digestion technique (Taylor, 1967). In many cases, dissections were made of uncleared specimens to confirm observations made on cleared specimens. Bone terminology follows Pietsch (1974a).

The generic diagnosis for females is based largely on osteological evidence presented elsewhere (Pietsch, 1974a). Generic and species descriptions are based on 116 metamorphosed females ranging from 11.0 to 170.0 mm (morphometrics and jaw tooth counts on specimens 20.0 mm and larger). Males and larvae were described by Bertelsen (1951:110–116). Study material is deposited in the following institutions:

AMNH: American Museum of Natural History, New York.
BMNH: British Museum (Natural History), London.
BOC: Bingham Oceanographic Collections, Peabody Museum of Natural History, Yale University.
IOM: Institute of Oceanology, Academy of Sciences of the USSR, Moscow.
IOS: Institute of Oceanographic Sciences, Surrey, England (formerly the National Institute of Oceanography).
ISH: Institut für Seefischerei, Hamburg.
LACM: Natural History Museum of Los Angeles County.
MCZ: Museum of Comparative Zoology, Harvard University.
MNLR: Musee d'Histoire Naturelle de La Rochelle.
NYZS: New York Zoological Society.
OSUO: Oregon State University, Department of Oceanography, Corvallis.
ROM: Royal Ontario Museum, Toronto.
SU: Stanford University (collections now housed at the California Academy of Sciences, San Francisco).
UMML: University of Miami Marine Laboratory.
USNM: United States National Museum, Washington.
UW: Fish Museum, University of Washington, Seattle.
ZMB: Zoological Museum, University of Bergen.
ZMUC: Zoological Museum, University of Copenhagen.

OSTEOLOGY

The osteology of *Chaenophryne* has been previously described in detail and compared with that of other oneirodid genera (Pietsch, 1974a; *C. melanorhabdus* misidentified as *C. parviconus*). Not mentioned before, however, is the conspicuous, honeycomblike network of ridges that partially form many of the bones of *Chaenophryne*. These highly cancellous bones include those that provide the dorsal surface of the cranium, excluding those that form the illicial trough: the dorsal surface of the frontals, the sphenotics, pterotics, parietals, and posttemporals; portions of the mandibular arch: the maxillaries, dentaries, and articulars; and parts of the opercular apparatus: the operculum, suboperculum, and preoperculum.

Osteological preparations were made of all four species of *Chaenophryne* using the trypsin digestion technique of Taylor (1967). Comparison of specimens of a similar size showed little interspecific vari-

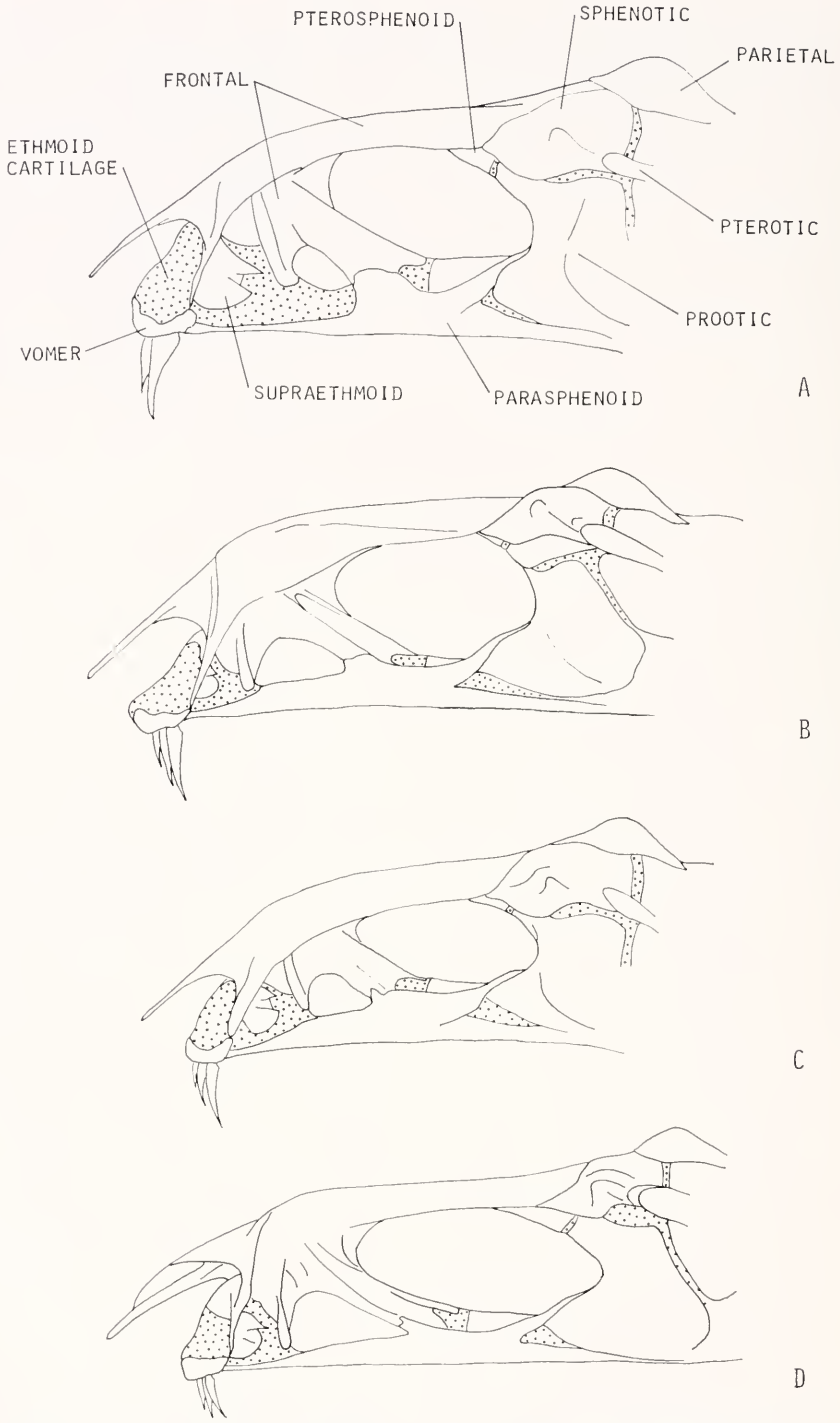


Figure 1. Lateral views of crania of *Chaenophryne*: A. *C. longiceps*, LACM 30196-26, 40.0 mm; B. *C. draco*, LACM 31436-2, 42.0 mm; C. *C. melanorhabdus*, LACM 34073-1, 35.0 mm; D. *C. ramifera*, MCZ 47556, 42.0 mm.

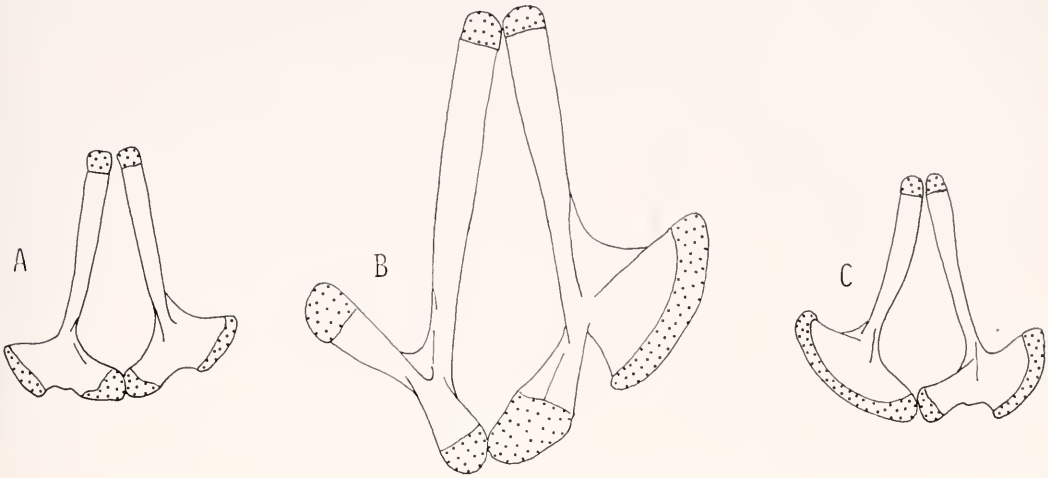


Figure 2. Pelvic bones of *Chaenophryne*: A. *C. draco*, LACM 34072-1, 33.0 mm; B. *C. melanorhabdus*, LACM 30619-5, 58.0 mm; C. *C. ramifera*, ISH 765/68, 35.0 mm.

ation. The cranium of *C. ramifera*, however, is considerably more elongate and depressed than that of its congeners (Fig. 1). This elongation and depression is mainly due to having longer frontal bones which are slightly concave on their dorsal surface compared to the dorsally convex frontals of all other species of *Chaenophryne*. As a result of this, the frontals of *C. ramifera* are in a more anterior position; the ventromedial extensions of these bones, which are by consequence longer than those of its congeners, help to form longer and considerably narrower orbital foramina.

In an earlier paper (Pietsch, 1974a:29, 30, 86, 89, fig. 56D, Table 23) I described *Chaenophryne* as having triradiate pelvic bones based on an examination of three cleared and stained specimens of *C. melanorhabdus* (59.0–96.0 mm; incorrectly referred to as *C. parviconus*). Examination of additional material of all four species of *Chaenophryne* by clearing and staining and by dissection, has shown that the pelvic bones vary in shape from triradiate to broadly expanded distally. In some cases, the two extremes of this variation may occur in the same specimen (Fig. 2).

SYSTEMATICS

Genus *Chaenophryne* Regan, 1925

Females:

Chaenophryne Regan, 1925:564 (type species *Chaenophryne longiceps* Regan, 1925, by original designation and monotypy).

Himantolophus Regan, 1926:40 (in part; type species *Himantolophus groenlandicus* Reinhardt, 1837, by monotypy; separate in 1837, see Reinhardt, 1838).

Males:

Rhynchoceratias Regan, 1926:44 (in part; type species *Rhynchoceratias brevirostris* Regan, 1925, by subsequent designation of Fowler, 1936).

Trematorhynchus Regan and Trewavas, 1932:91 (in part; type species *Rhynchoceratias leuchorhinus* Regan, 1925, by subsequent designation of Burton, 1933).

Diagnosis for females. The genus *Chaenophryne* is distinguished from all other genera of the family Oneirodidae by the absence of sphenotic spines, an operculum that is only slightly concave posteriorly, and highly cancellous bones (the latter not found in any other ceratioid). In addition, *Chaenophryne* is unique in having the following combination of characters: mouth

large, cleft extending past eye; dorsal profile of frontal bones strongly convex; anterior end of pterygiophore of illicium exposed (see generic description below), its posterior end concealed under skin; illicium length greater than 20 percent of SL; symphysial spine of lower jaw rudimentary; articular spines rudimentary; angular spine absent; vomerine teeth present; pharyngobranchial I absent; pharyngobranchials II and III present and toothed; epibranchial teeth absent; hypobranchial II present; pectoral lobe short and broad, shorter than longest rays of pectoral fin; suboperculum elongate, upper end tapering to a point, lower part nearly circular with anterior projection in some specimens; anal fin with 5 rays, rarely 4 or 6; skin naked, covering caudal fin to some distance from fin base.

Diagnosis for males. Nonparasitic; skin between nostrils and between posterior nostril and eye pigmented; 8 to 12 olfactory lamellae; upper denticular with 10 to 22, irregularly curved denticles, mutually fused in a semicircular group; lower denticular with 13 to 31, recurved denticles in 2 to 3 irregular series; skin black and naked; no teeth in jaws; shape of pectoral fin-lobe, opercular bones, and anal fin-ray counts as for females (taken largely from Bertelsen, 1951:109).

Generic description of females. Body relatively short, globular; jaws equal anteriorly; symphysial spine of lower jaw small to absent; oral valves well-developed; eye subcutaneous, appearing through a circular, translucent area of integument; gill opening oval in shape, situated posteroventrad to pectoral lobe; skin naked (embedded dermal spines cannot be detected microscopically in cleared and stained specimens); lateral line papillae as described for other oneirodids (Pietsch, 1969, 1972b, 1974a, b); ovaries paired; pyloric caeca absent.

Operculum triangular in shape, only slightly concave along posterior margin; suboperculum elongate, upper end tapering to a point, lower part nearly circular with small anterior projection in some specimens (Bertelsen, 1951:109, figs. 66, 67).

Illicium length 20.1 to 47.4 percent of SL, becoming longer proportionately with growth (Fig. 3); pterygiophore of illicium 70 to 82 percent of SL (less than 50 percent of SL in other oneirodids; Pietsch, 1974a: 18); anterior end of pterygiophore of preserved specimens usually concealed under skin within illicial trough, but capable of considerable forward extension (as in *Oneirodes* and ceratiids; Bertelsen, 1943, 1951:18); posterior end of pterygiophore concealed under skin; esca with a single (*C. draco*-group) or paired (*C. longiceps*), conical to elongate, anterior appendage or appendages, internally pigmented with one, or three, round, translucent windows at tip; a filamentous medial appendage or appendages present (*C. longiceps*) or absent (*C. draco*-group); a posterior appendage consisting of a swollen basal portion and a compressed distal crest bearing none to numerous filaments anteriorly or distally, with (*C. draco*-group) or without (*C. longiceps*) a pair of fringed, anterior lobes; one or two filamentous, anterolateral appendages on each side (*C. melanorhabdus* and *C. ramifera*); a paired series of filaments arising laterally from anterior base of escal bulb (*C. ramifera*); a subcutaneous, internally pigmented appendage emerging from base of esca and descending along anterior margin of illicial bone (extremely well-developed in some specimens of *C. ramifera*).

Teeth slender, recurved and all depressible, in overlapping sets as described for other oneirodids (Pietsch, 1972b:5, fig. 2; 1974a, b); teeth in lower jaw larger than those in upper jaw; number of teeth in upper jaw 21 to 51, lower jaw with 26 to 57 teeth; jaw teeth few and rudimentary in specimens smaller than approximately 18 mm SL; vomerine teeth 2 to 4 on each side, the longest outermost.

Color in preservation dark brown to black over entire external surface of body except for bulb and usually appendages of

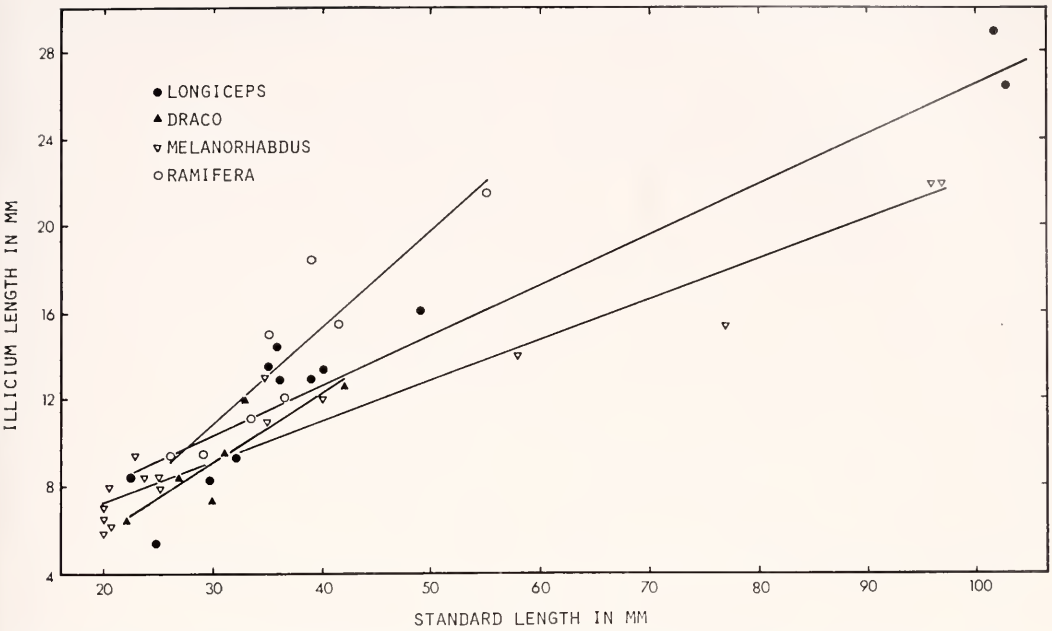


Figure 3. Graph of relationship of illicial length and standard length for species of *Chaenophryne*.

esca (see species accounts); oral cavity and guts except for outer surface of stomach wall unpigmented.

D. 6–8; A. 5–6; P. 16–22 (Table 2); pelvics absent; C. 9 (2 + 4 + 3); branchiostegal rays 6 (2 + 4).

Generic description of males. See Bertelsen (1951:110, 112, 116, figs. 66–70, 72, 73).

KEY TO FEMALES OF THE SPECIES OF THE GENUS CHAENOPHRYNE

The following key will differentiate adolescent and adult females only. For larvae and males see Bertelsen (1951:110).

1A. Esca with a pair of internally pigmented, anterior appendages; medial escal appendage or appendages present (Fig. 7); width of escal bulb 5.3–11.4 percent of SL in specimens 20 mm and larger (Fig. 4); pectoral fin-rays 17–22 rarely less than 18 (Table 2) ..... *C. longiceps* Regan, 1925.

1B. Esca with an unpaired, internally pigmented, anterior appendage; medial escal appendages absent (Figs. 8–10); width of escal bulb 2.1–6.6 in specimens 20 mm and larger (Fig. 4); pectoral fin-rays 16–19, rarely more than 18 (Table 2) ..... *C. draco*-group ..... 2.

2A. Esca without anterolateral appendages (Fig. 8); ratio of number of teeth in upper jaw to number of teeth in lower jaw 1.08–1.45 in specimens 20 mm and larger (Fig. 5) ..... *C. draco* Beebe, 1932.

2B. Esca with one to three anterolateral appendages on each side (Figs. 9, 10); ratio of number of teeth in upper jaw to number of teeth in lower jaw .76–1.30 (Fig. 5) ..... 3.

3A. Esca with a series of filaments arising laterally from anterior base of bulb (Fig. 10); ratio of number of teeth in upper jaw to number of teeth in lower jaw less than 1.00 in specimens 30 mm to approximately 60 mm (Fig. 5; specimens larger than 55.5 mm unknown); D. 8, rarely 7; A. 6, rarely 5; P. 17–19, rarely 16 (Table 2) ..... *C. ramifera* Regan and Trewavas, 1932.

3B. Esca without a series of filaments arising from base of bulb (Fig. 9); ratio of number of teeth in upper jaw to number of teeth in lower jaw greater than 1.05 in specimens 30 mm and larger (Fig. 5); D. 6–7, rarely 8; A. 5, rarely 6; P. 16–17, rarely 18 (Table 2) ..... *C. melanorhabdus* Regan and Trewavas, 1932.

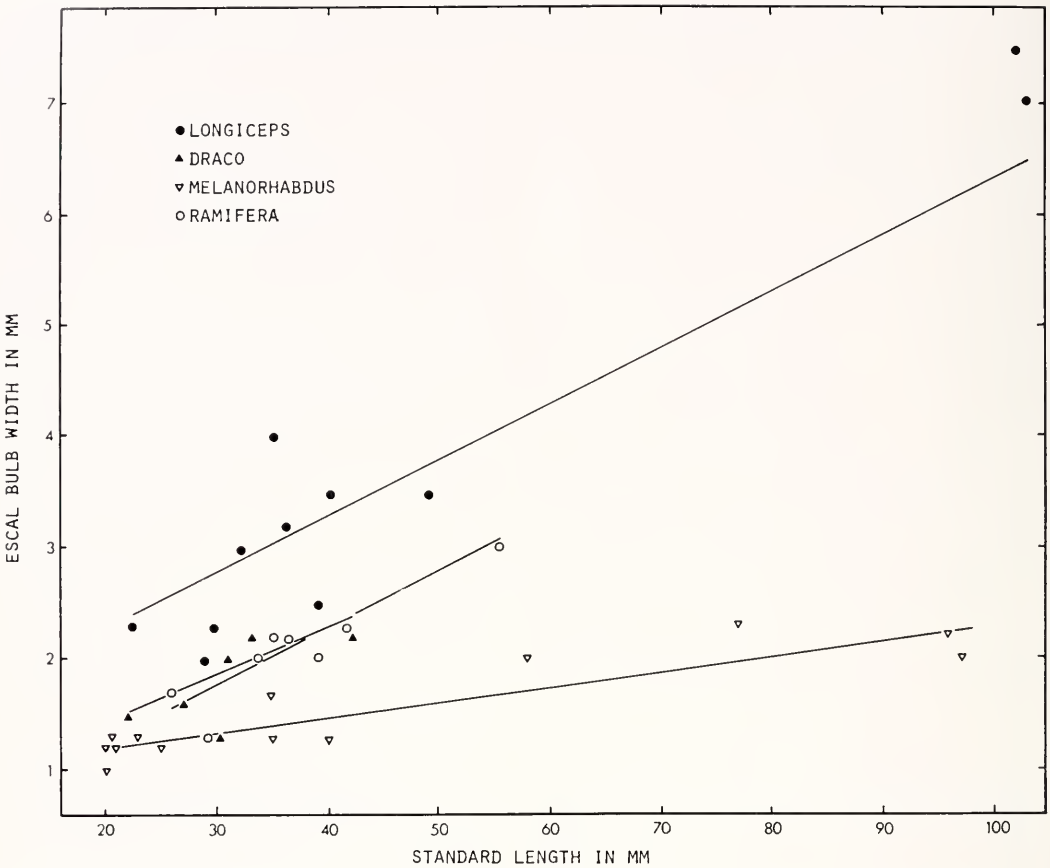


Figure 4. Graph of relationship of escal bulb width and standard length for species of *Chaenophryne*.

Chaenophryne longiceps Regan, 1925 Figures 6, 7

Chaenophryne longiceps Regan, 1925:564 (in part; original description; 14 specimens; lectotype, ZMUC P92106, 20.0 mm; DANA Station 1203 (11), 7°30′N, 79°19′W; 3000 m wire; 1500 hr; 11 January 1922). Regan, 1926:31, pl. 6, fig. 2 (in part; description after Regan, 1925; 3 additional specimens). Parr, 1927:22, fig. 8 (4 additional specimens designated *longiceps forma typica,* var. *quadrifilis* n. var., and var. *quadrifilis* ?; description). Regan and Trewavas, 1932:85, 86, figs. 14, 135 (description; lectotype designated as only representative of *longiceps*, 13 paralectotypes made types of

Table 2. Fin-ray frequencies for metamorphosed females of species of *Chaenophryne*.

	Dorsal			Anal		Pectoral						
Species	6	7	8	5	6	16	17	18	19	20	21	22
longiceps	4	14		16	2		1	4	5	5	4	1
draco	3	16	2	20	1	5	16	5				
melanorhabdus	4	14	1	16	2	6	11	2				
ramifera		2	10	2	10	1	7	3	1			

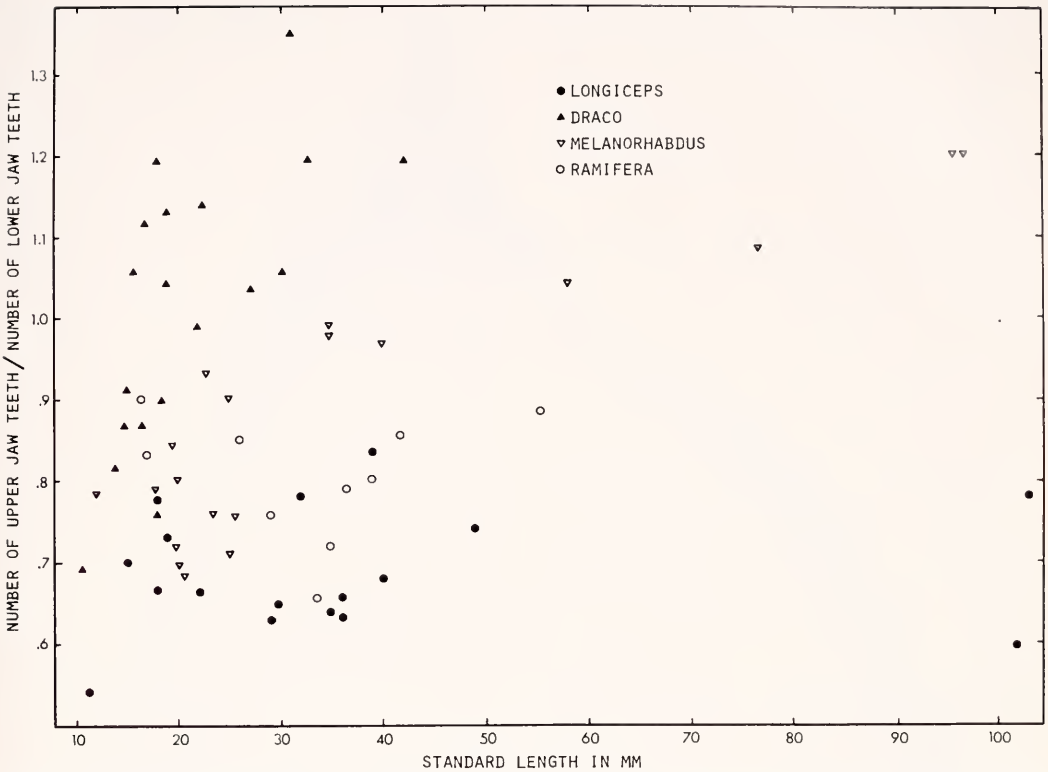


Figure 5. Graph of relationship of ratio between number of upper and lower jaw teeth, and standard length for species of *Chaenophryne*.

other species; in key). Bertelsen, 1951:111, 113, figs. 66A, 71, Table 23 (description; comparison with all known material; in key). Grey, 1956: 256 (synonymy; distribution). Pietsch, 1974a: 33 (listed).

Himantolophus groenlandicus, Regan, 1926:40 (in part; larval female referred to *longiceps*-group by Bertelsen, 1951).

Rhynchoceratias leuchorhinus, Regan, 1926:44 (in part; 2 males referred to *longiceps*-group by Bertelsen, 1951).

Chaenophryne crossotus Beebe, 1932:83, fig. 21 (original description; single specimen; holotype USNM 170942 (originally NYZS 20809), 17.0 mm; Bermuda Oceanographic Expedition, Net 1015, 32°12′N, 64°36′W; 0–915 m; 15 June 1931). Regan and Trewavas, 1932:85, 86 (*crossata;* description after Beebe, 1932; in key). Bertelsen, 1951:111, 114, Table 23 (*crossota;* description; comparison with all known material; in key). Grey, 1956·257 (*crossota;* synonymy; distribution). Pietsch, 1974a:33 (listed).

Chaenophryne bicornis Regan and Trewavas, 1932: 84, 85, fig. 133 (original description; 2 specimens; lectotype, ZMUC P92107, 14.0 mm; DANA Station 4005 (1), 13°31′N, 18°03′W; 4000 m wire; 1145 hr; 12 March 1930). Bertelsen, 1951:111, 113, fig. 66C, Table 23 (description; comparison with all known material; lectotype designated; in key). Grey, 1956:256 (synonymy; distribution). Pietsch, 1974a:33 (listed).

Chaenophryne crenata Regan and Trewavas, 1932: 84, 86, fig. 134 (original description; single specimen; holotype, ZMUC P92108, 18.0 mm; DANA Station 3714 (10), 15°22′N, 115°20′E; 2000 m wire; 0245 hr; 20 April 1929). Bertelsen, 1951:111, 114, fig. 66B, Table 23 (description; comparison with all known material; in key). Grey, 1956:257 (synonymy; distribution). Pietsch, 1974a:33 (listed).

Chaenophryne quadrifilis Regan and Trewavas, 1932:85, 87, fig. 136 (original description based on *longiceps quadrifilis* n. var. of Parr, 1927; 4 specimens; lectotype, BOC 2910 (not 2007 as in

Parr, 1927), 20.5 mm; PAWNEE Station 58, 32°24′N, 64°29′W; 3050 m wire; 20 April 1927). Parr, 1937:63 (listed; lectotype designated). Koefoed, 1944:8, pl. I, figs. 2, 3 (description of additional specimen). Bertelsen, 1951:111, 113, Table 23 (description; comparison with all known material; in key). Grey, 1956:257 (synonymy; distribution). Pietsch, 1974a:33 (listed).

Chaenophryne haplactis Regan and Trewavas, 1932:85, 87, fig. 137 original description; single specimen; holotype, ZMUC P92114, 11.0 mm; DANA Station 1152 (3), 30°17′N, 20°44′W; 3000 m wire; 1930 hr; 22 October 1921).

Trematorhynchus leuchorhinus, Regan and Trewavas, 1932:91 (in part; 2 males referred to *longiceps*-group by Bertelsen, 1951).

Chaenophryne longiceps-group Bertelsen, 1951:71, 110–114, 269, figs. 30, 66, 68–71, Table 23 (osteological description of larval female; 5 nominal species grouped; common characters; all available material listed; description of larvae, males, metamorphosing females; in key). Grey, 1956:256 (after Bertelsen, 1951; synonymy; distribution). Pietsch, 1974a:33 (after Bertelsen, 1951; included species listed).

Material. Thirty-three metamorphosed females, 11.0–170.0 mm: BMNH 1 (14.0 mm); BOC 3 (20.0–21.0 mm); IOM 1 (23.0 mm); IOS 1 (22.5 mm); ISH 4 (35.0–103.0 mm); LACM 2 (18.0–40.0 mm); MCZ 3 (17.0–39.0 mm); OSUO 1 (25.0 mm); ROM 1 (170.0 mm); SU 1 (36.0 mm); UMML 2 (19.0–49.0 mm); USNM 7 (13.5–29.5 mm); ZMB 1 (25.0 mm); ZMUC 5 (11.0–19.5 mm).

In addition to material listed by Bertelsen (1951:269) the following males have been examined: IOS 1 (11.0 mm); LACM 1 (12.0 mm); MCZ 2 (14.0–17.0 mm); USNM 1 (19.5 mm).

Diagnosis. In addition to characters of the esca which separate *C. longiceps* from all other species of *Chaenophryne* (see Key and Generic description), this species can be further distinguished from *C. draco* and *C. melanorhabdus* by having a smaller ratio between the number of upper and lower jaw teeth (Fig. 5). The illicium of *C. longiceps* appears to be slightly shorter than that of *C. ramifera* and slightly longer than that of *C. melanorhabdus* (Fig. 3). *Chaenophryne longiceps* has fewer dorsal and anal fin-rays than *C. ramifera*, and a greater number of pectoral fin-rays than all other species of the genus (Table 2).

Description. Esca with a pair of elongate, internally pigmented (except for tip) and bilaterally placed, anterior appendages (occasionally sharing a common base as in holotype of *C. crenata;* Regan and Trewavas, 1932:86, fig. 134), less than one-tenth to greater than length of escal bulb; one to three, transversely placed, medial appendages, bifurcated at midlength to highly filamentous from base, darkly pigmented in some large specimens (102.0 and 103.0 mm); medial appendages may arise at any point from distal surface of escal bulb to anterior margin of swollen basal portion of posterior appendage (Fig. 7); a posterior appendage consisting of a swollen basal portion and a membranous, distal crest, darkly pigmented in largest known specimens (102.0–170.0 mm), and bearing one to several filaments anteriorly or distally in some specimens; anterolateral appendages and basal series of filaments absent; in most specimens a subcutaneous, internally pigmented descending appendage (Fig. 7).

Illicial length 22.4–40.3 percent of SL (Fig. 3); escal bulb width 5.3–11.4 percent of SL (Fig. 4); total number of teeth in upper jaw 28–40, in lower jaw 34–57; ratio of number of teeth in upper jaw to number in lower jaw .70–.94 (Fig. 5); vomerine teeth 4–8; D. 6–8; A. 5–6; P. 17–22 (Table 2).

Rest of characters as for genus.

Distribution. Chaenophryne longiceps has a wide horizontal distribution, occurring in all three major oceans of the world. It has been collected from both sides of the north Atlantic from the equator to the northern coast of Iceland. Three records are known from the Indo-Pacific region: in the Indian Ocean from the Arabian Sea (approximately 7°N, 65°E) and Bay of Bengal (9°N, 90°E), and from the South China Sea. In the eastern Pacific, records extend from as far west as the Hawaiian Islands, between approxi-

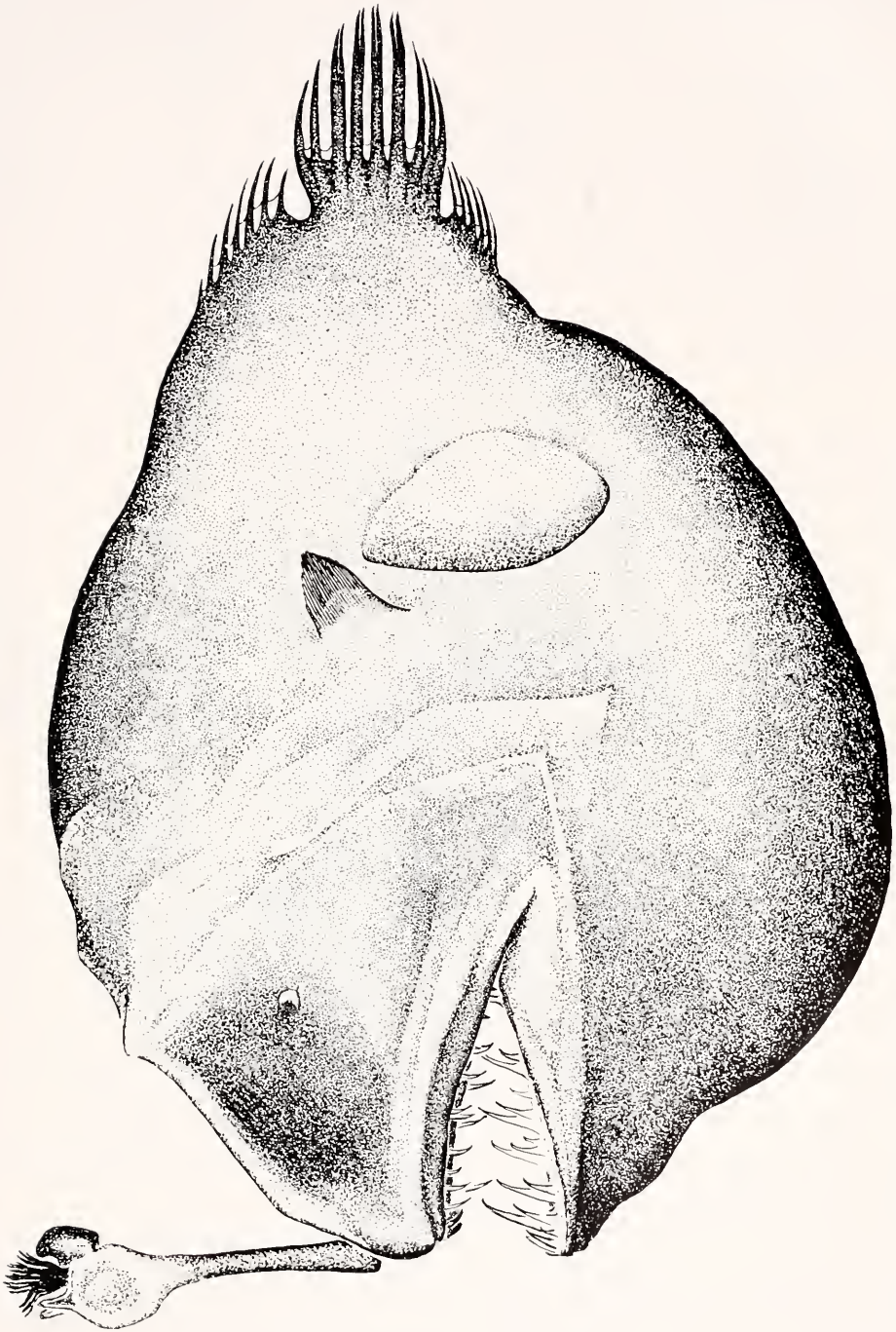


Figure 6. *Chaenophryne longiceps*, ISH 237/73, 102.0 mm. Drawn by Elizabeth Anne Hoxie.

Figure 7. Escae of *Chaenophryne longiceps*: A. MCZ 47561, 17.0 mm, left side; B. IOS uncatalogued, 22.5 mm, left side; C. MCZ 49854, 29.0 mm, left side; D. MCZ 49857, 39.0 mm, left side; E. ISH 237/73, 102.0 mm, anterior view; F. ISH 607/73, 103.0 mm, left side.

mately 45°N off the coast of Oregon and 23°S off Chile. The lectotype of *C. longiceps* was collected from the Gulf of Panama (Fig. 11).

Based on maximum depths reached by fishing gear, metamorphosed female specimens of *C. longiceps* are vertically distributed between approximately 500 m and an unknown lower limit. Eighty-eight percent of the known material (28 in-

dividuals) was captured by gear fished below 850 m. The largest known specimens (3 individuals, 102.0–170.0 mm) were captured by nets fished below 950 m. Material is not sufficient from any one geographic area for a more analytical treatment of distributional data.

Comments. Bertelsen (1951) proposed the *Chaenophryne longiceps*-group to include five nominal species described by Beebe (1932) and Regan and Trewavas (1932) on the basis of one to four adolescent female specimens less than 25 mm, and on relatively small differences in the morphology of the esca. The greater amount of material now available, providing some understanding of individual and ontogenetic variation, has shown that these differences in escal morphology must be regarded as variation exhibited by widely distributed conspecific populations. In the absence of significant differences, these forms are here synonymized with *C. longiceps* (Table 1).

Chaenophryne haplactis, known only from the holotype (11.0 mm), was placed in the *C. draco*-group by Bertelsen (1951) on the basis of absence of inner pigment on the caudal peduncle and a low pectoral fin-ray count (15 according to Regan and Trewavas, 1932). Re-examination of the holotype by Bertelsen (personal communication) shows the somewhat bleached remains of large, stellate melanophores on the peduncle; I count 18 pectoral rays. Further, the esca of this specimen clearly has the paired anterior appendages characteristic of *C. longiceps* (Regan and Trewavas, 1932:89, fig. 137). For these reasons, *C. haplactis* is removed from the *C. draco*-group and placed within the synonymy of *C. longiceps.*

Chaenophryne draco-group Bertelsen, 1951
Figures 8–10

Himantolophus groenlandicus, Regan, 1926:40 (in part; 2 larval females referred to *draco*-group by Bertelsen, 1951).

Rhynchoceratias leuchorhinus, Regan, 1926:44 (in part; 3 males referred to *draco*-group by Bertelsen, 1951).

Trematorhynchus leuchorhinus, Regan and Trewavas, 1932:91 (in part; 5 males referred to *draco*-group by Bertelsen, 1951).

Chaenophryne draco-group Bertelsen, 1951:72, 110, 114–118, 270, figs. 30, 67, 72–75, table 23 (osteological description of adolescent male; 3 nominal species grouped; common characters; all available material listed; description of larvae, males, metamorphosing females; in key). Grey, 1956:257 (after Bertelsen, 1951; synonymy; distribution). Maul, 1962:22, fig. 10 (description of metamorphosing female). Pietsch, 1974a:33 (after Bertelsen, 1951; included species listed).

Material. Metamorphosed female specimens are listed below by species. In addition to material listed by Bertelsen (1951: 270), the following males of the *C. draco*-group have been examined: IOM 2 (12.5–15.0 mm); IOS 16 (10.5–14.0 mm); LACM 7 (9.5–13.5 mm); MCZ 5 (7.0–14.5 mm).

Comments. The *Chaenophryne draco*-group (Bertelsen, 1951) is retained to include larvae and males readily separated from those of *C. longiceps* by larval pigmentation and pectoral fin-ray counts, but not divisible into smaller taxonomic units. Within the *C. draco*-group are also included three species based on metamorphosed females that together differ from *C. longiceps* in the basic design of the esca (see Key, Generic description and Figs. 7–10), and in other characters listed in the key to species. These three species are associated with the larvae and males of the *C. draco*-group by retention of the characteristic larval pigmentation in small specimens, and by pectoral fin-ray counts (Bertelsen, 1951: 110; Table 3).

Chaenophryne draco Beebe, 1932
Figure 8

Chaenophryne longiceps Regan, 1925:564 (in part; original description; 14 specimens; paralectotypes of *longiceps* subsequently made types of *parviconus, columnifera, melanodactylus* by Regan and Trewavas, 1932). Regan, 1926:31 (in part; after Regan, 1925).

Chaenophryne draco Beebe, 1932:84, fig. 22 (original description; single specimen; holotype, USNM 170943 (originally NYZS 22396), 16.5 mm; Bermuda Oceanographic Expedition Net 1181, 32°12′N, 64°36′W; 1100 m; 15 August 1931). Regan and Trewavas, 1932:85, 89 (description after Beebe, 1932; in key). Bertelsen, 1951:115, 116, Table 24 (description; comparison with all known material; in key). Grey, 1956:258 (synonymy; distribution). Pietsch 1974a:33 (listed).

Chaenophryne parviconus Regan and Trewavas, 1932:35, 85, 87, figs. 39, 41, 138 (original description, osteology of head, pectoral arch; 9 specimens; lectotype, ZMUC P92110, 12.5 mm; DANA Station 1209(2), 7°15′N, 78°54′W; 3000 m wire; 1845 hr; 17 January 1922). Beebe and Crane, 1947:158 (6 additional specimens; description; *columnifera* and *melanorhabdus* synonyms of *parviconus*). Bertelsen, 1951:115, 117, fig. 74B, C (in part; description; comparison with all known material; in key; *haplactis, atriconus, columnifera, melanodactylus, macractis, melanorhabdus, pterolophus, pacis* synonyms of *parviconus*). Grey, 1956:258 (synonymy; distribution). Pietsch, 1974a:33 (listed).

Chaenophryne atriconus Regan and Trewavas, 1932:85, 87, fig. 139 (original description; single specimen; holotype, ZMUC P92111, 15.0 mm; DANA Station 3847(5), 12°02′S, 96°43′E; 1500 m wire; 2100 hr; 11 October 1929).

Chaenophryne columnifera Regan and Trewavas, 1932:85, 88, fig. 140 (original description; 3 specimens; lectotype hereby designated, ZMUC P92112, 14.5 mm; DANA Station 1208(15), 6°48′N, 80°33′W; 2600 m wire; 1715 hr; 16 January 1922).

Chaenophryne melanodactylus Regan and Trewavas, 1932:85, 88, fig. 141 (original description; single specimen; holotype, ZMUC P92116, 15.0 mm; DANA Station 1370(13), 36°36′N, 26°14′W; 3000 m wire; 1150 hr; 13 June 1922).

Chaenophryne macractis Regan and Trewavas, 1932:85, 88, fig. 142 (original description; single specimen; holotype, ZMUC P92115, 14.0 mm; DANA Station 3561(4), 4°20′S, 116°46′W; 2000 m wire; 0900 hr; 24 September 1928).

Material. Forty-six metamorphosed females. 11.0–42.0 mm: AMNH 2 (29.0–35.0 mm); BMNH 5 (12.0–14.0 mm); IOS 1 (30.0 mm); LACM 17 (13.0–42.0 mm); MCZ 4 (12.5–18.0 mm); NYZS 6 (13.5–19.5); USNM 1 (16.5 mm); ZMUC 10 (11.0–15.0 mm).

Diagnosis. In addition to the characters of the esca, which separate *C. draco* from all other species of *Chaenophryne* (see Key and Generic description), this species is distinguished by having the highest ratio between the number of upper and lower jaw teeth of any species (Fig. 5). The illicium of *C. draco* appears to be slightly shorter than that of *C. ramifera* and slightly longer than that of *C. melanorhabdus* (Fig. 3). Fewer pectoral fin-rays, and fewer dorsal and anal rays, help to distinguish *C. draco* from *C. longiceps* and *C. ramifera*, respectively (Table 2).

Description. Esca with a single conical to elongate, internally pigmented (except for tip), anterior appendage, less than one-seventh to nearly one-third length of escal bulb; medial appendages absent; a posterior appendage consisting of a swollen basal portion, and a somewhat compressed distal crest with a posterior filament or filaments and a pair of anterior lobes each bearing none to numerous filaments; anterolateral appendages and basal series of filaments absent; in larger specimens, a subcutaneous, internally pigmented, descending appendage (Fig. 8).

Illicial length 24.0–36.4 percent of SL (Fig. 3); escal bulb width 4.3–6.7 percent of SL (Fig. 4); total number of teeth in upper jaw 35–47, in lower jaw 31–38; ratio of number of teeth in upper jaw to number in lower jaw 1.08–1.45 (Fig. 5); vomerine teeth 4–8; D. 6–8; A. 5–6 (of 21 specimens only one had A. 6); P. 16–18 (Table 2).

Rest of characters as for genus.

Distribution. Chaenophryne draco has a wide horizontal distribution, occurring in all three major oceans of the world. It has been collected from both sides of the Atlantic: two specimens from off Bermuda (including the holotype), one from the Cape Verde Islands, and a fourth from 36°36′N, 26°14′W. Four records are known from the Indo-Pacific region: two on the equator at approximately 65°E, one from off the Cocos Islands (12°02′S, 96°43′E), and one from Sagami Bay, Japan (*C.*

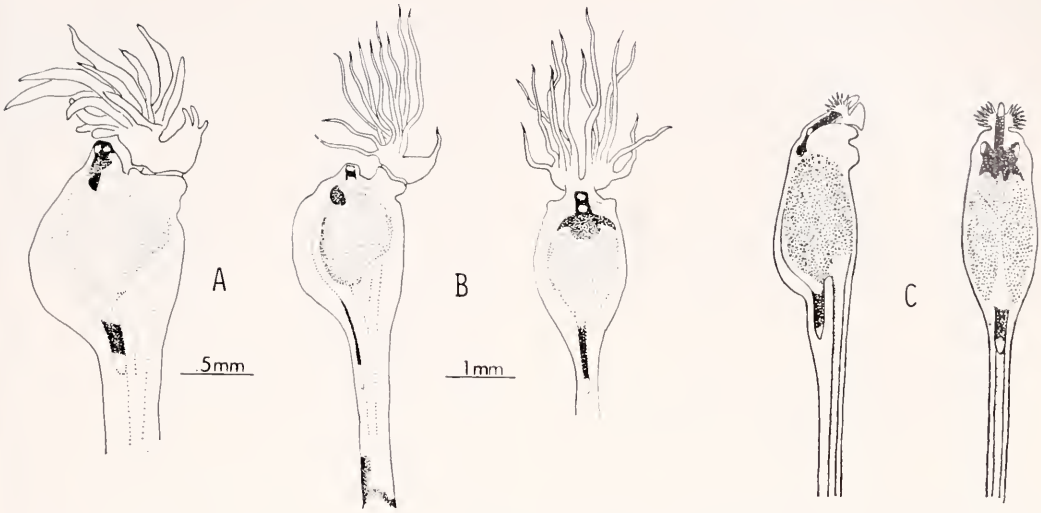


Figure 8. Escae of *Chaenophryne draco*: A. MCZ 49863, 12.5 mm, left side; B. holotype of *C. macractis*, ZMUC P92115, 15.0 mm, lateral and anterior views reversed from Regan and Trewavas, 1932; C. LACM 32788-2, 19.0 mm, left lateral and anterior views.

macractis of Imai, 1942). In the western Pacific, records extend from the Hawaiian Islands (13 specimens) to the Gulf of Panama (18 records), between approximately 21°N and 4°S (Fig. 11).

Based on maximum depths reached by fishing gear, metamorphosed female specimens of *C. draco* are vertically distributed between approximately 350 m and an unknown lower limit. Eighty-nine percent of the known material (42 individuals) was captured by gear fished below 700 m. Sufficient material is known from the Gulf of Panama for analysis of vertical data by a procedure outlined by Gibbs (1969; see Methods and Materials). Results indicate a concentration between 700 and 1500 m (Table 3).

Comments. Prior to his monograph on the Ceratioidei, Bertelsen (1951) had not seen the holotype of *C. draco* Beebe, 1932. Beebe's (1932:85, fig. 22) colorful description and somewhat stylized figure of the esea did not fully agree with descriptions of other species introduced six months later by Regan and Trewavas (1932). These forms were maintained as separate species pending examination of Beebe's type. Personal examination of the holotype of *C. draco* (16.5 mm) has confirmed Bertelsen's (1951) prediction that *C. parviconus* (and

Table 3. Vertical distribution of *Chaenophryne draco* based on specimens collected by the DANA in the Gulf of Panama. Meter-hours and specimens expressed as percent of total. See text for methods of calculation.

Depth (m)	Meter-hours	Specimens
0–100	16.5	0
101–200	5.9	0
201–300	0.1	0
301–400	15.4	0
401–500	0	–
501–600	2.4	0
601–700	0	–
701–800	1.6	5.6
801–900	0	–
901–1000	5.9	11.1
1001–1250	10.7	27.7
1251–1500	8.9	50.0
1501–1750	14.5	5.6
1751–2000	11.2	0
2001–3000	5.9	0
3000	0	–
Number of specimens		18
Number of meter-hours	596.6	
Number of hauls	83	

most of its included synonyms; see Table 1) is a junior synonym of *C. draco*.

Chaenophryne melanorhabdus Regan and Trewavas, 1932
Figure 9

Chaenophryne melanorhabdus Regan and Trewavas, 1932:85, 89, fig. 143 (original description; single specimen; holotype, ZMUC P92117, 40.0 mm; DANA Station 1203(14), 7°30′N, 79°19′W; 2500 m wire; 2030 hr; 11 January 1922).

Chaenophryne pterolophus Regan and Trewavas, 1932:85, 89, fig. 144 (original description; single specimen; holotype, ZMUC P92118, 20.5 mm; DANA Station 1208 (16), 6°48′N, 80°33′W; 2100 m wire; 1715 hr; 16 January 1922).

Chaenophryne parviconus, Grinols, 1966:161–165, fig. 1, Tables 1, 2 (misidentification; 2 specimens; description; escae figured; distribution). Pietsch, 1972a:35, 36, 42, 45, fig. 24(6) (misidentification; osteological comments; otolith described, figured). Pietsch, 1974a:33, 109, figs. 26, 37, 39D, 46, 49, 51F, 52B, 56D (misidentification; osteological description; comparison with other oneriodid genera; phylogenetic relationships).

Material. Twenty-three metamorphosed females, 11.0–97.0 mm: LACM 18 (11.0–97.0 mm); SU 1 (20.0 mm); UW 2 (39.0–68.0 mm); ZMUC 2 (20.5–40.0 mm).

Diagnosis. The characters of the esca easily separate *C. melanorhabdus* from all other species of *Chaenophryne* (see Key and Generic description). In addition, the ratio between the number of upper and lower jaw teeth is less than that of *C. draco* but significantly greater than that of *C. longiceps* and *C. ramifera* (Fig. 5). The illicium of *C. melanorhabdus* is shorter than that of its congeners (Fig. 3). Finally, fewer pectoral fin-rays, and fewer dorsal and anal rays, help to distinguish *C. melanorhabdus* from *C. longiceps* and *C. ramifera*, respectively (Table 2).

Description. Esca with a single, elongate, internally pigmented (except for tip), anterior appendage, less than one-fourth to nearly one-third length of escal bulb; medial appendages absent; a posterior appendage consisting of a swollen basal portion and a somewhat compressed, distal crest with a posterior filament or filaments and a pair of anterior lobes each bearing numerous filaments; a filamentous, anterolateral appendage on each side; basal series of filaments absent; subcutaneous, internally pigmented, descending appendage well-developed, often extending full length of illicium (Fig. 9).

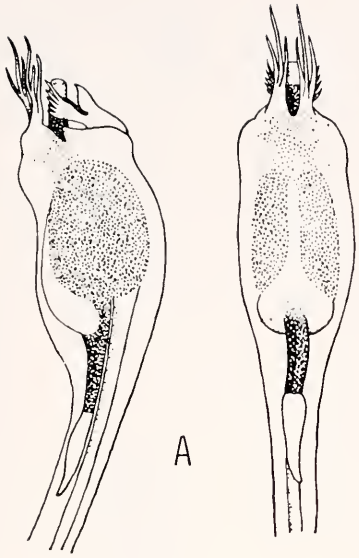
Illicial length 20.1–41.3 percent of SL (Fig. 3); escal bulb width 2.1–6.3 percent of SL (Fig. 4); total number of teeth in upper jaw 21–45, in lower jaw 26–42; ratio between number of teeth in upper jaw to number of teeth in lower jaw .78–1.30 (Fig. 5); vomerine teeth 4–7; D. 6–8 (of 19 specimens only one had D. 8); A. 5–6; P. 16–18 (Table 2).

Rest of characters as for genus.

Distribution. Chaenophryne melanorhabdus appears to be restricted to the western continental slope of North and Central America, ranging from approximately 46°N, 125°W in Pacific Subarctic Water, through the mixed Transition Zone of the California Current (18 specimens), into the Eastern Pacific Equatorial waters of the Gulf of Panama (type locality) (Fig. 11).

Based on maximum depths reached by fishing gear, metamorphosed female specimens of *C. melanorhabdus* are vertically distributed between approximately 200 m and an unknown lower limit. Eighty-three percent of the known material (19 individuals), including the largest specimens (35.0 mm and larger) was collected by gear fished below 450 m. Sufficient material is known from the Transition Zone of the California Current for analysis of vertical data by a procedure outlined by Gibbs (1969; see Methods and Materials). Results indicate a concentration between 300 and 1000 m (Table 4).

Comments. Beebe and Crane (1947:158) synonymized *C. melanorhabdus* and *C. columnifera* with *C. parviconus* considering the material to represent stages of development. Bertelsen (1951:114, 117) agreed



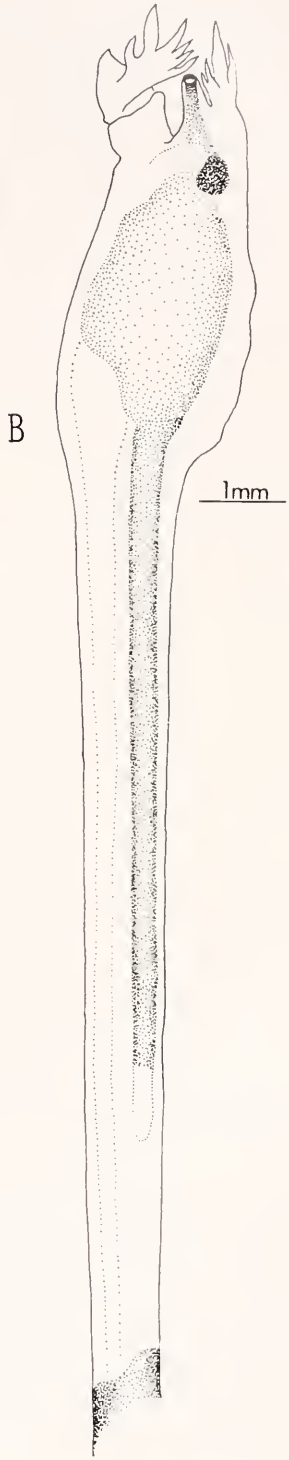


Figure 9. Escae of *Chaenophryne melanorhabdus*: A. holotype of *C. melanorhabdus*, ZMUC P92117, 40.0 mm, lateral and anterior views reversed from Regan and Trewavas, 1932; B. LACM 30387-1, 96.0 mm, left side, showing extent of subcutaneous descending appendage.

with this action and the reasons for it, adding a number of additional forms to the synonymy of *C. parviconus*, including *C. pterolophus* (Table 1). Recent collecting in the Eastern Pacific especially by the VELERO IV of the Allan Hancock Foundation and the University of Southern California, has yielded a number of specimens of *Chaenophryne*, including a complete growth series (12.0–97.0) that have a pair of filamentous, anterolateral escal appendages like those present in Regan and Trewavas' (1932) *C. melanorhabdus* and *C. pterolophus*. In all other characters this new material compares very well with the type material. Consequently, *C. melanorhabdus*, with *C. pterolophus* as a junior synonym, is removed from the synonymy of *C. pariconus* and given specific status.

Chaenophryne ramifera Regan and Trewavas, 1932
Figure 10

Chaenophryne ramifera Regan and Trewavas, 1932:85, 90, fig. 146 (original description; single specimen; holotype, ZMUC P92119, 17.0 mm; DANA Station 3550(6), 7°10′N, 78°15′W; 3000 m wire; 0145 hr; 5 September 1928). Belloc, 1938:305, fig. 29 (after Regan and Trewavas, 1932; comparison with *C. intermedia* sp. nov.). Bertelsen, 1951:115, figs. 67D, 75, Table 24 (description; comparison with all known material; in key; *fimbriata*, *intermedia* synonyms of *ramifera*). Pietsch, 1974a:33 (listed).

Chaenophryne fimbriata Regan and Trewavas, 1932:85, 90, fig. 145 (original description; single specimen, holotype, ZMUC P92120, 16.5 mm; DANA Station 3917(3), 1°45′N, 71°05′E; 3200 m wire; 1800 hr; 5 December 1929). Belloc, 1938:305, fig. 27 (after Regan and Trewavas, 1932; comparison with *C. intermedia* sp. nov.).

Chaenophryne intermedia Belloc, 1938:305, figs. 24, 28 (original description; single specimen; holotype, MNLR P449, 14.0 mm; PRÉSIDENT THÉODORE TISSIER Station 708, 14°54′N, 23°15′W; 1000 m wire; 15 May 1936).

Chaenophryne pacis Koefoed, 1944:9, pl. II, figs. 6, 7 (original description; single specimen; holotype, ZMB 4301, 15.0 mm; MICHAEL SARS Station 53, 34°59′N, 33°01′W; 2600 m wire; 8–9 June 1910).

Table 4. Vertical distribution of *Chaenophryne melanorhabdus* based on specimen collected by the VELERO IV off southern California. Meter-hours and specimens expressed as percent of total. See text for methods of calculation.

Depth (m)	Meter-hours	Specimens
0–100	4.3	0
101–200	2.1	0
201–300	6.3	0
301–400	7.7	16.7
401–500	5.2	11.1
501–600	6.5	16.7
601–700	8.2	33.3
701–800	8.2	0
801–900	8.3	0
901–1000	6.0	11.1
1001–1250	14.4	0
1251–1500	17.7	11.1
1501–1750	3.4	0
1751–2000	1.1	0
2001–3000	0.7	0
3000	0	–
Number of specimens		18
Number of meter-hours	10143.7	
Number of hauls	547	

Material. Fifteen metamorphosed females, 13.5–55.5 mm: IOM 1 (16.0 mm); ISH 5 (26.0–55.5 mm); MCZ 3 (13.5–39.0 mm); MNLR 1 (14.0 mm); UMML 1 (36.5 mm); ZMB 1 (15.0 mm); ZMUC 3 (16.5–33.5 mm).

Diagnosis. The characters of the esca distinguish *C. ramifera* from all other species of *Chaenophryne* (see Key and Generic description). In addition, the low ratio between the number of upper and lower jaw teeth further separates this species from *C. draco* and *C. melanorhabdus* (Fig. 5). The illicium of *C. ramifera* is longer than that of its congeners (Fig. 3). *Chaenophryne ramifera* has fewer pectoral fin-rays than *C. longiceps*, and a greater number of dorsal and anal rays than all other species (Table 2).

Description. Esca with a single, elongate, internally pigmented, anterior appendage, approximately one-fourth to nearly one-

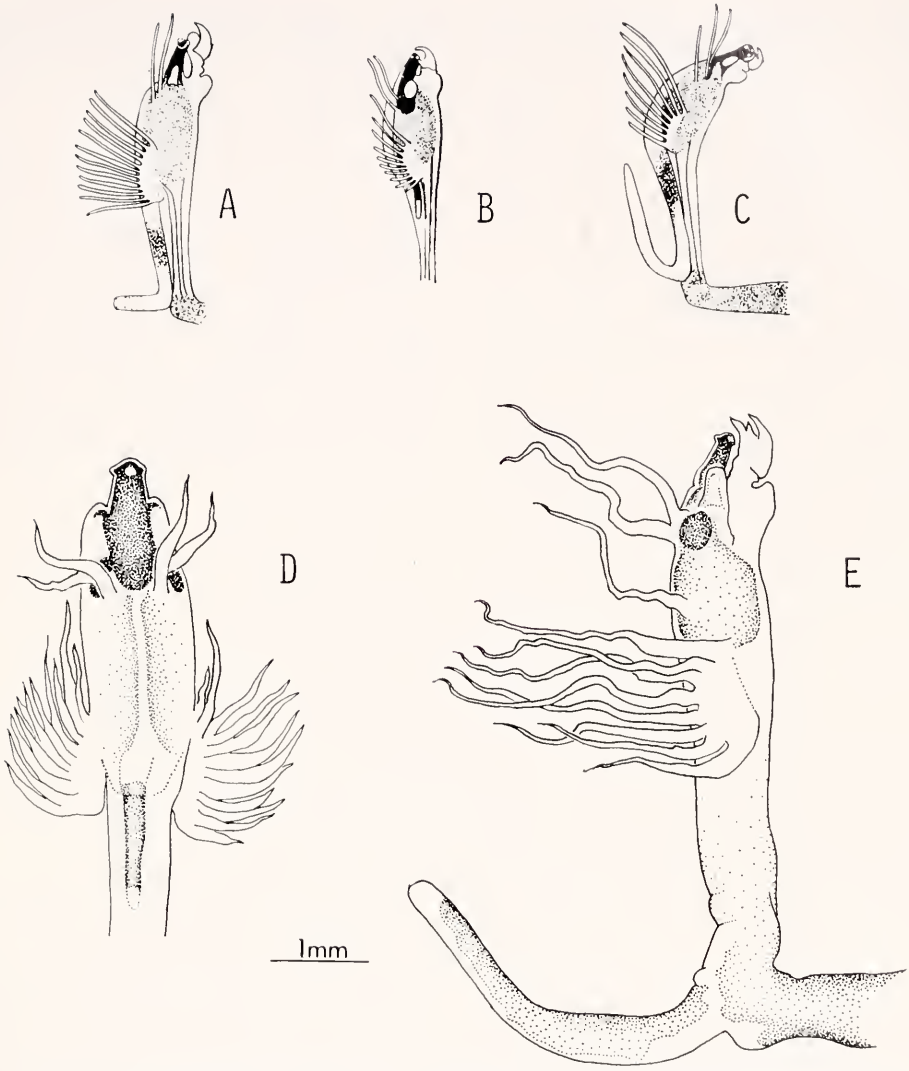


Figure 10. Escae of *Chaenophryne ramifera*: A. holotype of *C. intermedia*, MNLR P449, 14.0 mm, lateral view reversed from Belloc, 1938; B. holotype of *C. fimbriata*, ZMUC P92120, 16.5 mm, lateral view reversed from Regan and Trewavas, 1932; C. holotype of *C. ramifera*, ZMUC P92119, 17.0 mm, lateral view reversed from Regan and Trewavas, 1932; D. ISH 2247/71, 26.0 mm, anterior view; E. UMML 29702, 36.5 mm, left side.

third length of escal bulb, trilobed distally with three round translucent windows; anterior appendage flanked laterally by an elongate, unpigmented swelling; medial appendages absent; a posterior appendage consisting of a swollen basal portion and a somewhat compressed distal crest with a terminal, anteriorly directed, crescent-shaped filament and a pair of anterior lobes each bearing none to several filaments; two or three, filamentous, anterolateral appendages on each side; a basal series of seven to twelve filaments on each side; subcutaneous, internally pigmented, descending appendage extremely well-developed in some specimens (see Comments below), emerging as a free, anteriorly and dorsally directed tentacle (Fig. 10).

Illicial length 32.8–47.4 percent of SL (Fig. 3); escal bulb width 4.5–6.5 percent of SL (Fig. 4); total number of teeth in upper jaw 25–51, in lower jaw 33–53; ratio between number of teeth in upper jaw to number of teeth in lower jaw .76–.98 (Fig. 5); vomerine teeth 4–8; D. 7–8; A. 5–6; P. 16–19 (of 15 specimens only one had P. 16 and one had P. 19) (Table 2).

Rest of characters as for genus.

Distribution. Chaenophryne ramifera has a wide horizontal distribution occurring in all three major oceans of the world. In the Atlantic it appears to be restricted to the eastern side; the northern and westernmost record is at approximately 35°N, 33°W (the holotype of *C. pacis*); seven additional specimens were collected between approximately 11°N and 8°S, between 26°W and 4°E in the Gulf of Guinea. In the Indo-Pacific region, five records are known ranging across the Indian Ocean between 9°N and 2°S. The holotype, collected from the Gulf of Panama, is the only known specimen from the Pacific Ocean (Fig. 11).

Based on maximum depth reached by fishing gear, metamorphosed female specimens of *C. ramifera* are distributed vertically between approximately 200 m and an unknown lower limit. Large specimens may be captured at relatively shallow depths: a 35.0 mm specimen was collected by gear fished above 200 m, a 36.5 mm specimen by gear fished above 550 m. Eighty-seven percent of the known material (13 individuals) was captured by gear fished below 550 m, 47 percent (7 individuals) by gear fished below 1000 m. Material is not sufficient from any one geographic area for a more analytical treatment of distributional data.

Comments. I have not seen the holotype of *C. pacis*. From Koefoed's (1944:9, fig. 6, 7) description and figures, there can be little doubt that this is a synonym of *C. ramifera*. The anterolateral appendages and basal series of filaments have apparently been lost; but the "trilobed stigma" unique to *C. ramifera*, with its three translucent windows at the tip of the unpaired anterior escal appendage, is well-developed. *Chaenophryne pacis* is removed from the synonymy of *C. parviconus* and placed within that of *C. ramifera*.

The development of the subcutaneous, descending escal appendage of *C. ramifera* does not appear to be correlated with ontogeny as thought by Bertelsen (1951:118). Of the 15 known specimens of this species, only five have an esca with the descending appendage emerging as a free tentacle. These five specimens range from 13.5 mm to 36.5 mm. In all other known individuals the descending appendage is quite short, only 16.3 percent of the illicial length in the largest known specimen (55.5 mm).

Species Incertae Sedis

Chaenophryne galeatus Koefoed, 1944, nomen nudum.

Chaenophryne galeatus Koefoed, 1944:8.

Comments. This name was used by Koefoed in a manuscript dated 1918 (not seen by me), and later mentioned in published form (Koefoed, 1944:8) without application to a description or type.

EVOLUTIONARY RELATIONSHIPS

Chaenophryne is unique in several ways and does not appear to be phylogenetically closely related to any other oneirodid genus (see Pietsch, 1974a:89, fig. 104). Evolutionary relationships among the species of *Chaenophryne* are deduced on the basis of eight morphological characters chosen for their intraspecific stability and interspecific variability. These characters are summarized below with a discussion of the evolutionary direction of each. Methods used in determination of directional change in character states follow Pietsch (1974a). For each character the primitive state is given a lower case letter, the derived state a capital letter, and a secondary derivation, a capital letter starred.

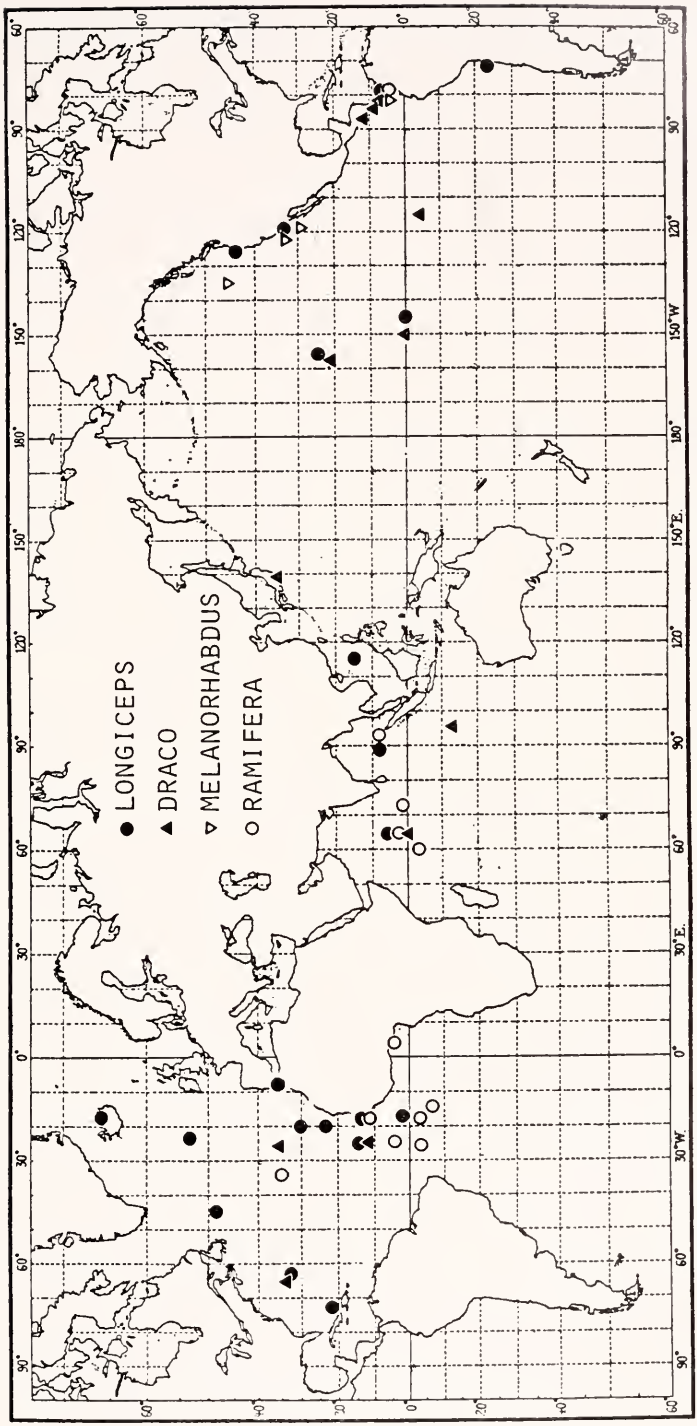


Figure 11. Chart showing known geographical distribution of species of *Chaenophryne*. A single symbol may represent more than one capture.

1. Length and shape of frontal bones. Elongation and depression of the frontals is a general trend found within the family Oneirodidae and within several of its contained genera (*Dolopichthys*, *Oneirodes*; Pietsch, 1972b, 1974a). The relatively short, dorsally convex frontals of *C. longiceps*, *C. draco*, and *C. melanorhabdus* (Fig. 1A–C) are considered to represent a primitive state (a); the longer, dorsally concave frontals of *C. ramifera* (Fig 1D) are a derived condition (A).

2. Anterolateral escal appendages. Within more speciose oneirodid genera (*Dolopichthys*, *Oneirodes*; Pietsch, 1972b, 1974a) there is a trend toward an increase in morphological complexity of the esca. The absence of anterolateral appendages in *C. longiceps* and *C. draco* (Figs. 7, 8) is a primitive condition (b); whereas, the presence of these appendages in *C. melanorhabdus* and *C. ramifera* (Figs. 9, 10) represents a derived condition (B).

3. Basal series of escal filaments. The absence of a series of filaments arising from the base of the escal bulb in *C. longiceps*, *C. draco*, and *C. melanorhabdus* (Figs. 7–9) is a primitive condition (c); presence of this series in *C. ramifera* (Fig. 10) is a derived state (C).

4. Escal bulb width. The width of the escal bulb of *C. longiceps* (Fig. 4) is like that of nearly all other ceratioids and is thought to represent a primitive condition (d). The considerably narrower bulb of *C. draco*, *C. melanorhabdus*, and *C. ramifera* (Fig. 4) is considered a derived state (D).

5. Illicial length. Elongation of the illicium is a trend found in several oneirodid genera (*Dolopichthys*, *Oneirodes*, *Lophodolos*; Pietsch, 1972b, 1974a, b). The short illicium of *C. melanorhabdus* represents a primitive condition (e), an illicium of intermediate length found in *C. longiceps* and *C. draco* represents a derived state (E), and the relatively long illicium of *C. ramifera* a further derived state (E*; Fig. 3).

6. Pectoral fin-rays. The loss of fin-rays is a general trend found within the Ceratioidei. Among species of *Chaenophryne* two character states are recognized: 18–22, rarely 17 (*C. longiceps*) (f); 16–18, rarely 19 (*C. draco*, *C. melanorhabdus*, *C. ramifera*) (F; Table 2).

7. Dorsal and anal rays. The loss of fin-rays is a general trend found within the Ceratioidei. Among species of *Chaenophryne* two character states are recognized: D. 8, rarely 7, A. 6, rarely 5 (*C. ramifera*) (g); D. 6–7, rarely 8, A. 5, rarely 6 (*C. longiceps*, *C. draco*, *C. melanorhabdus*) (G; Table 2).

8. Ratio between number of upper and lower jaw teeth. Nearly all ceratioids have a greater number of teeth in the lower jaw relative to the number of teeth in the upper jaw, resulting in a low ratio between these two counts. The low ratio found in *C. longiceps* and *C. ramifera* is considered a primitive state (h). The considerable higher ratio found in *C. draco* and *C. melanorhabdus* is the derived state (H; Fig. 5).

A hypothetical phylogeny for the species of *Chaenophryne* was constructed on the basis of shared patterns of derived character states. Each level in the phylogeny (Fig. 12) represents the maximum number of shared derived states for the maximum number of taxa (Pietsch, 1974a:87). For comparison of the four species with respect to evolutionary specialization, the following numbers were assigned to the character states: 0 = lower case letter, 1 = capital letter, 2 = capital letter starred. The maximum index of specialization is 9. The actual totals for the taxa are: *longiceps* 2, *draco* 5, *melanorhabdus* 5, *ramifera* 7. The

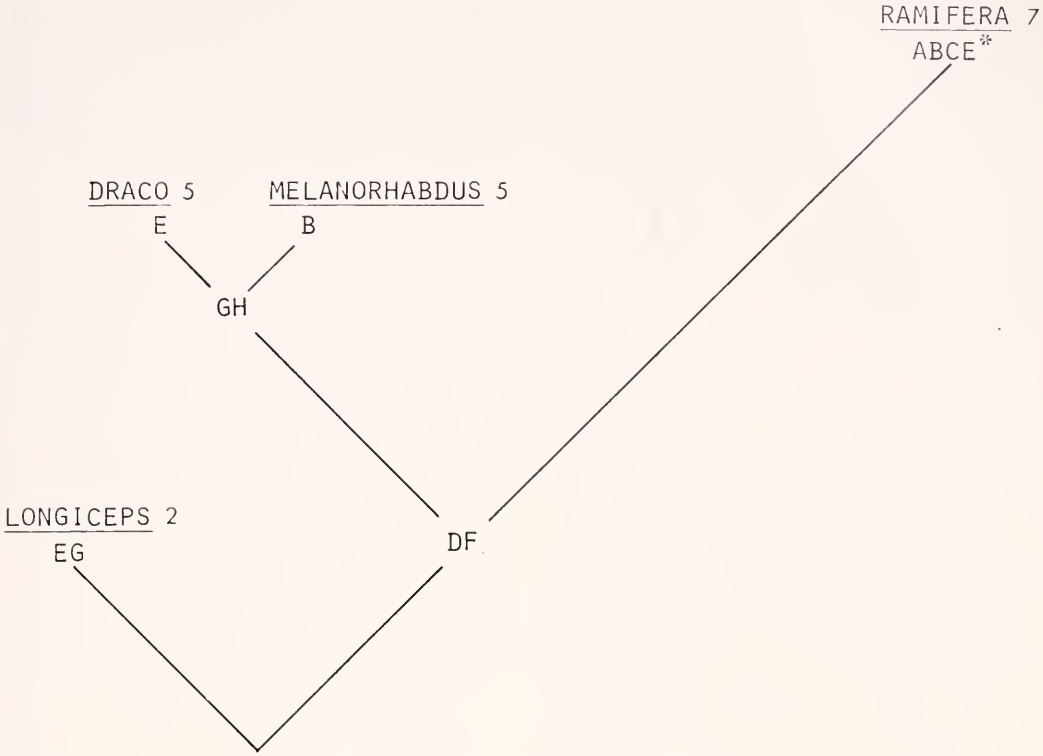


Figure 12. Proposed phylogenetic relationships of species of *Chenophryne*. Each level in the phylogeny represents the maximum number of shared derived character states for the maximum number of taxa. See text for details.

length of the line between any two levels in the phylogeny (Fig. 12) corresponds to the degree of evolutionary specialization found between those two levels. For example, the distance from the base of the phylogeny to ABCE* is seven units long, equalling the sum of the values of evolutionary specialization assigned to advanced character states DFABCE*. The number of derived character states shared between all possible species pairs of *Chaenophryne* is summarized in Table 5.

From this character analysis, it appears that *C. longiceps* is the least derived member of the genus having the least number of derived character states; it is most closely related to *C. draco* with which it shares a greater number of derived states than any other species. *Chaenophryne ramifera* is the most derived species, having the greatest number of derived character states; it is most closely related to *C. melanorhabdus* with which it shares a greater number of derived states than any other species. *Chaenophryne draco* and *C. melanorhabdus* are more closely related to each other than to any other species, sharing the greatest number of derived character states of any species pair (Table 5).

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TABLE 5. NUMBER OF DERIVED CHARACTER STATES SHARED BETWEEN ALL POSSIBLE SPECIES PAIRS OF *CHAENOPHRYNE*. NUMBERS IN PARENTHESES REFER TO CHARACTERS SUMMARIZED IN THE TEXT.

Species pair	Number of derived states shared
draco-melanorhabdus	4(4, 6–8)
melanorhabdus-ramifera	3(2, 4, 6)
longiceps-draco	2(5, 7)
draco-ramifera	2(4, 6)
longiceps-melanorhabdus	1(7)
longiceps-ramifera	0

J. Nelson (AMNH); Alwyne Wheeler (BMNH); Keith S. Thomson (BOC); William N. Eschmeyer and Tomio Iwamoto (California Academy of Sciences, San Francisco); Thomas A. Clarke (Hawaii Institute of Marine Science, University of Hawaii); T. S. Rass and N. V. Parin (IOM); Nigel Merrett and Julian Badcock (IOS); Gerhard Krefft (ISH); Robert J. Lavenberg and Jerry W. Neumann (LACM); Robert G. Schoknecht (MCZ); Michael Legand (Office de la Recherche Scientifique et Technique Outre-Mer, Nouméa, New Caledonia); William G. Pearcy (OSUO); W. B. Scott (ROM); Catherine Rainwater (University of Southern California, Los Angeles); C. Richard Robins and Robert N. Lea (UMML); Robert H. Gibbs, Jr. and Stanley H. Weitzman (USNM); Richard H. Backus, James E. Craddick and Bruce H. Robinson (Woods Hole Oceanographic Institution); A. P. Andriashev (Zoological Institute, Academy of Sciences of the USSR, Leningrad); Hans Kauri (ZMB); and Erik Bertelsen (ZMUC). In addition, I am grateful to Andrea West for typing the manuscript, and to Elizabeth Anne Hoxie for her excellent rendering of Figures 6, 7E and F.

For gracious hospitality extended to me during visits to their institutions, I am particularly grateful to Erik Bertelsen (ZMUC); Gerhard Krefft (ISH); Nigel Merrett and Julian Badcock (IOS); and Alwyne Wheeler (BMNH).

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The American orb-weaver genera *Larinia*, *Cercidia* and *Mangora* north of Mexico (Araneae, Araneidae)

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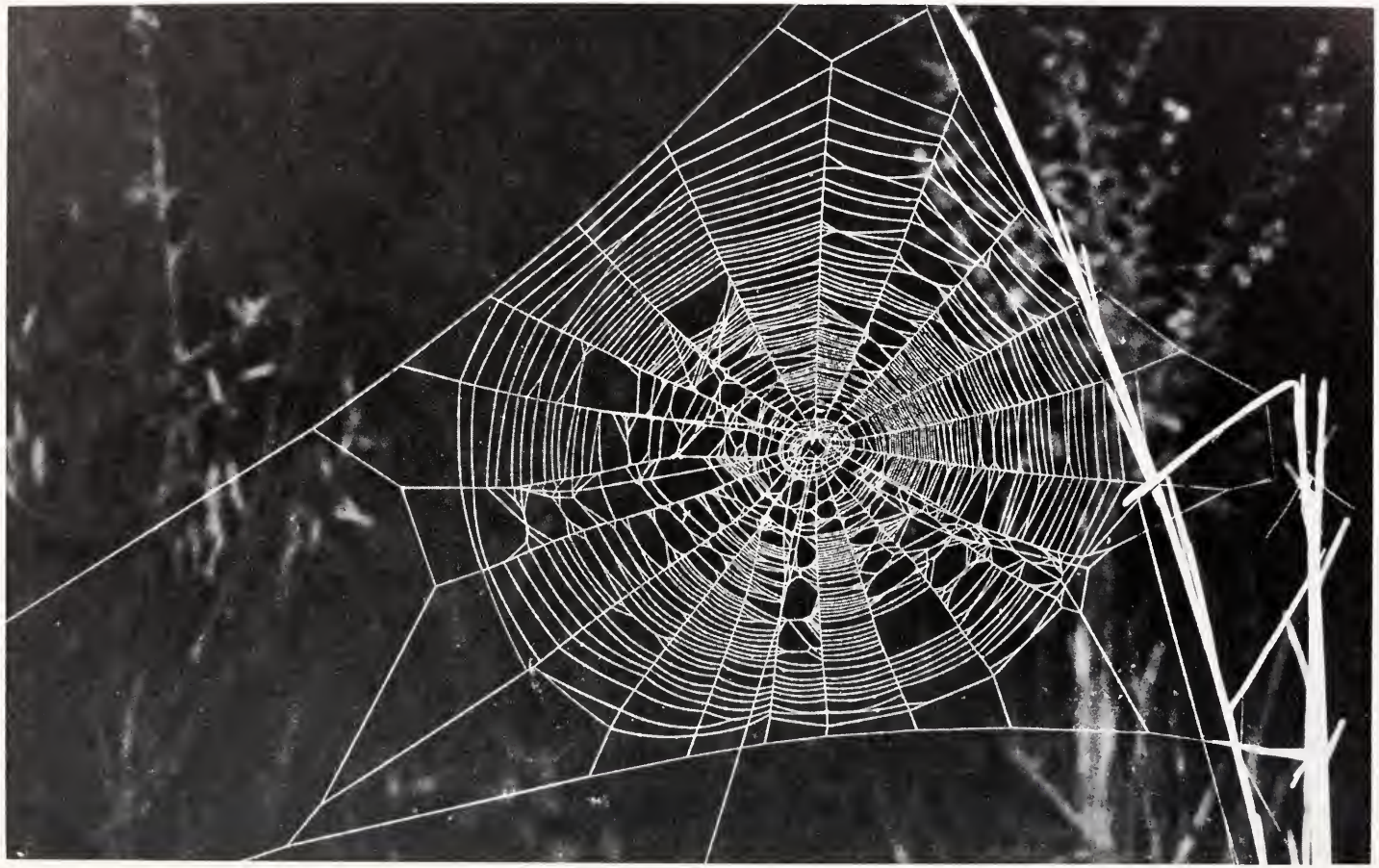

Frontispiece. Web of *Larinia directa* dusted with cornstarch and photographed at night by W. G. Eberhard (Carimagua, Meta, Colombia).

THE AMERICAN ORB-WEAVER GENERA *LARINIA*, *CERCIDIA* AND *MANGORA* NORTH OF MEXICO (ARANEAE, ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. There are three species of *Larinia* found north of Mexico, one of which, *Larinia directa,* occurs as far south as southern Brazil. The closest relatives are found in Africa. *Cercidia prominens,* possibly introduced from Europe, is found from the Great Lakes region to New England in relatively undisturbed habitats. *Cercidia* and *Larinia* are closely related offshoots of *Araneus.*

While *Mangora* species are found in all parts of the world, most are Neotropical. Of the seven species of *Mangora* found north of Mexico, three are tropical.

As a result of the discovery that *Cercidia funebris* is an older name for *Hypsosinga singaeformis,* this rarely used name must be changed to *H. funebris.*

INTRODUCTION

Revisionary studies of invertebrates try to accomplish several different tasks. The first task is to analyze a group of species and genera so that they can be arranged in phylogenetic order; the second is to devise a guide for the determination of the species; and the third, to discover generalizations of interest to biology. The first two aims are somewhat contradictory, since, in order to provide an ideal phylogenetic system, the group should be studied worldwide.

Nevertheless, I have limited myself to the American fauna because a worldwide study would make the determination of the spiders in North America exceedingly cumbersome, as well as greatly delaying the publication of the results. An additional problem, which does not plague students of vertebrates, is the difficulty of obtaining sufficient museum specimens of the genera under study, because most collections are not and cannot be sorted to genera. But for nonspecialists to be able to determine spiders of North America is an urgent necessity, as arachnologists all have teaching, research, and curatorial obligations, and do not have time to determine all the specimens submitted by entomologists interested in insect ecology and insect predators. Ironically, a taxonomic revision sometimes is the stimulus for swamping its author with requests for determinations of the studied species.

To facilitate determinations the taxonomic studies of the American orb-weavers will be published in two series: first, the species of araneid genera north of Mexico; later, the very many more species from the rest of the Americas. For the purposes of determination, it is obviously much easier to keep the fauna of America north of Mexico distinct from the rich tropical fauna. However, it is difficult to revise North American species without reference to tropical species and the better known temperate species of Europe. Even though I am limiting this work to the Araneidae of northern parts of North America, I am examining and illustrating all the types of species names from other parts of America to minimize later changes and to get a better idea of the diversity of species and

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genera. Unfortunately, many of these types are known from only one sex or from immatures. Of course, I am also examining specimens from other parts of the world, as they can be found in American collections.

Perhaps it is the broader aspect of the study, the revision of the genera within the family, that makes me uneasy about using the small genera in Grasshoff's excellent studies (1970a, b, c), even though each is a natural group of closely related species. Pending better knowledge of spiders, it may be better and easier to keep genera large. Also, judging from my study, it appears that *Larinia* and *Cercidia* are very closely related to *Araneus*, but *Mangora* is a specialized group far removed from *Araneus*. Nevertheless, for this paper, and until I know more about the groups, I will keep *Larinia* and *Mangora* together, following Simon (1895) and Grasshoff.

Larinia does not rest in the center of the web, but on vegetation to the side, as do most other relatives of *Araneus*. *Mangora* rests in the hub, and, like many other Araneidae that rest in the center (e.g., *Argiope*, *Gasteracantha*, *Acanthepeira*, *Cyclosa*, *Leucauge* and *Micrathena*), is more specialized in structure. Why there should be a relationship between the resting place and the appearance of the spider I do not know, except perhaps for the obvious explanation that an exposed spider would be more subjected by predators to selection pressure favoring inconspicuousness or the ability to disappear rapidly.

Specimens for this study were made available by J. A. Beatty of the Southern Illinois University, D. Bixler, J. E. Carico, R. E. Crabill of the U. S. National Museum, C. D. Dondale of Canadian National Collections, A. Timotheo da Costa of the Museu Nacional, Rio de Janeiro, H. Dybas of the Field Museum of Natural History, W. J. Gertsch of the American Museum of Natural History, M. Grasshoff of Senckenberg Naturmuseum, M. Hubert of Muséum National d'Histoire Naturelle, Paris, D. Lowrie, W. Peck of the Exline-Peck collection, S. Riechert, V. D. Roth, R. X. Schick of the California Academy of Sciences, W. Sedgwick, K. Stone, W. Staręga of the Polish Academy of Science, F. Wanless and D. Norman of the British Museum (Natural History), H. V. Weems of the Florida State Collection of Arthropods. T. Kronestedt of the Natural History Museum, Stockholm, provided information, and F. Enders transmitted specimens from South American museums. Lorna R. Levi corrected the syntax. The study and its publication were supported in part by National Science Foundation research grant GB-36161.

Larinia Simon

Larinia Simon 1874, Arachnides de France, 1: 115. Type species by monotypy *Epeira lineata* Lucas, 1846. The gender of the generic name is feminine.

Drexelia McCook, 1892, Proc. Acad. Natur. Sci. Philadelphia 1892: 127. Type species by monotypy *Epeira directa* Hentz.

In several excellent studies, Grasshoff (1970a, b, c, 1971) split *Larinia* into numerous genera (*Kilima, Larinopa, Siwa, Paralarinia, Faradja, Mahembea, Lariniaria*), each including related species. But if I were to follow Grasshoff, I would have to make additional new genera for the tropical American species. Perhaps the Grasshoff genera should be considered subgenera (Grasshoff, in letter). Even this would be unsatisfactory, however, as it is not possible to express all phylogenetic relationships through nomenclature. For the time being I prefer to use *Larinia* in its broad sense.

The type species of *Larinia* Simon is *L. lineata,* occurring in the Mediterranean region. It has recently been illustrated by Grasshoff (1970b), as have most species other than American ones. In this discussion I refer to the various papers of Grasshoff.

Description. Larinia species are elongate, the abdomen longer than wide, often pointed anteriorly above the carapace and projecting behind and above spinnerets

(Figs. 5, 6). Behind the median eyes the yellowish carapace may have a double line that fuses to a single median longitudinal line. The legs are not banded, but may have ventral and sometimes dorsal black spots. The sternum may be all black, or may have the sides but not the anterior black. The abdomen has a pattern, usually variable within a species, of longitudinal lines, sometimes with two rows of black spots; the sides are white. The venter of the abdomen is gray to black, the dark area surrounds the spinnerets. Anteriorly, the dark area encloses a longitudinal white patch that is often divided by a median black line (Figs. 6, 16, 25). The height of the clypeus equals about the diameter of the anterior median eyes. The carapace has a median longitudinal thoracic line more pronounced in males. There are four teeth on the anterior margin of each chelicera.

Genitalia. The female epigynum has a scape, which I think is torn off in specimens I have examined of *L. lineata* of the Old World. The internal genitalia have a duct connecting the large opening with the seminal receptacles (Figs. 9, 12, 19, 28, and illustrations of Grasshoff's papers). Along the duct are numerous, irregularly placed, kernel-like structures, each connected with the lumen of the connecting duct. Presumably these structures are glands that have the outer layer sclerotized.

The embolus of the palpus is ribbon-shaped with the edge facing mesally, the broad side apically. The embolus tip breaks off during mating and stays behind in the female duct [Figs. 31–33 and Grasshoff, 1970a, fig. 1f for *Larinia* (*Kilima*) *conspersa;* 1970b, fig. 7d for *Larinia chloris;* 1971, fig. 33d for *Larinia* (*Drexelia*) *trifida;* fig. 38b for *Larinia* (*Drexelia*) *bifida;* and fig. 44a for *Larinia* (*Drexelia*) *ishango.*] The tip contains a duct (Figs. 31–33). The palpus has a median apophysis projecting to the side of the palpus, a subterminal apophysis and a terminal apophysis (Fig. 3). I am not certain that I have been consistent in naming the subterminal apophysis in various genera. There is a hematodocha between embolus and radix, and a large distal hematodocha between the sclerotized portion of the terminal and subterminal apophysis and the embolus. In *Kilima,* according to Grasshoff, tegulum and stipes are fused. The structure of the male palpus is so similar to that of *Araneus* that I believe *Larinia* is close to *Araneus.* If this is the case, the tip or cap of the embolus, which breaks off during mating, probably has a lumen in *Araneus* too. Grasshoff found a lumen in the embolus tip of *Araneus,* but I have been unable to confirm its presence in this more sclerotized structure.

Diagnosis. Besides having diagnostic ventral coloration very different from that of *Araneus* and *Metepeira* (which has a white median ventral longitudinal band framed by black), *Larinia* differs from *Araneus* by the eye arrangement. The anterior median eyes are the largest, separated by more than one diameter; the posterior median eyes are subequal to anterior medians or slightly smaller (to 0.8 diameter), and are almost touching or are separated from each other by their radius at most. The anterior median eyes are 1.2 to 1.5 diameters apart. The median ocular quadrangle is more than twice as wide in front as behind (Figs. 5, 15, 24).

Males are smaller than females and have longer legs. In males of American species the palpal femur has a basal ventral tooth (as in *Araneus*); the palpal patella has two long macrosetae (one in *Kilima,* Grasshoff, 1970a); the first coxa lacks a hook (but has one in *Kilima*); the first or second legs have stronger macrosetae than in the female.

Note. Several South American *Eustala* species resemble *Larinia,* including the commonest one, *E. fuscovittata.* However, the genitalia differ; the *Eustala* epigynum has an anteriorly directed scape and the palpus has a large, nonsclerotized median apophysis parallel to the long axis of the appendage. The closeness of the posterior

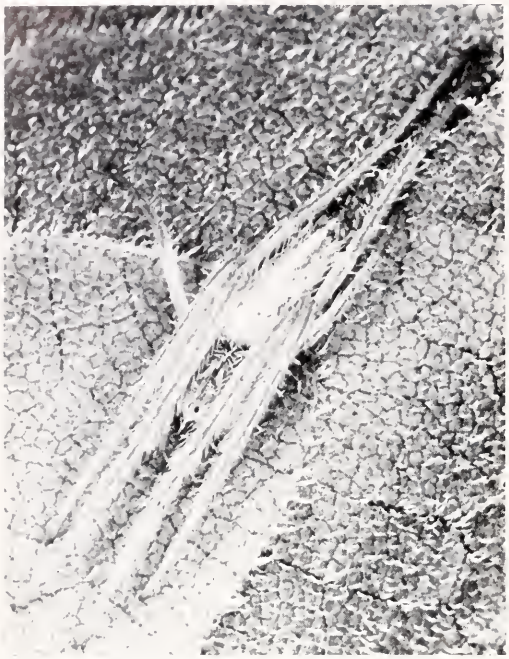


Plate 1. *Larinia directa*, penultimate female, from North Carolina in the laboratory.

median eyes to each other may be an adaptation to the leg position of the resting animal (Plate 1).

Relationship. I believe this genus is close to *Araneus* but not to *Mangora*. *Larinia* lacks the high carapace and the feathered trichobothria characteristic of *Mangora*, and the structure of the genitalia differs considerably. Traditionally *Larinia* has been placed close to *Mangora*. Archer (1951b: 26) also considered *Larinia* close to *Araneus*.

Grasshoff (1971) shows that the species closest to the North American ones are found in Africa. I assume that of the three species found north of Mexico, *Larinia directa*, with a range extending from southern Brazil to southern United States, is the ancestral one. *Larinia borealis* and *L. famulatoria* appear to be two temperate species, one eastern, one western, derived from *L. directa*. Now the ranges of all three overlap in the southwestern United States.

Natural History. Specimens of *Larinia* are commonly collected by sweeping. *Larinia directa* is found in open areas; it sits in the hub of the web at night and in vegetation to the side of the web by day. (Frontispiece and W. Eberhard, personal communication).

Distribution. Worldwide but absent from central and northern Europe.

Misplaced species. Larinia forata Keyserling 1893 (= *Epeira forata* McCook 1893) is *Araneus niveus* (Hentz). NEW SYNONYMY. The specimen has a Marx label "*Epeira muraria* Mx, Sta. Rosa, Cala. no. 442" and a pencil label by McCook *Epeira forata*. The locality appearing in the publication and on the label is in error; *Araneus niveus* and close relatives are not found in California. The specimen is in the United States National Museum.

Larinia nigrofoliata Keyserling, 1884 = *Araneus miniatus* (Walckenaer, 1841).

Separating species. The three species found in the Nearctic area differ in proportions, size, and in the genitalia (the base and scape of the epigynum, and the shape of the embolus). The palpus is similar and lightly sclerotized in all three species, and the median apophysis has greater variation within each species than among the three species (Figs. 37–46).

Key to American Species of *Larinia* North of Mexico

1 First patella and tibia of female 1.6 to 2.2 times carapace length, distal rim of epigynal scape wide and smooth (Figs. 7, 10, 11); first patella and tibia of male 2.0 to 2.4 times carapace length, New Jersey, Arkansas, southern Arizona, southern California to southern Brazil (Map 1). ..... *directa*

– First patella and tibia of female 1.2 to 1.6 times carapace length, distal rim of scape not wide and smooth (Figs. 17, 20, 21, 26); first patella and tibia of male 1.4 to 1.7 times carapace length. 2

2(1) Sternum black, venter of abdomen with black marks (Fig. 25); females with transverse striations on base of scape, and lateral lip of epigynal base diagonal (Figs.

Map 1. Distribution of *Larinia directa* (Hentz).

26, 29, 30); total length of males less than 3.3 mm; Wyoming, Idaho, southern California to Chiapas (Map 2). ..... *famulatoria*

– Sternum with sides black at darkest, venter of abdomen with gray marks (Fig. 16); females with striations of scape curved posteriorly at middle, and lateral lip of epigynal base framing opening laterally and posteriorly forming a right angle (Figs. 17, 20, 21); total length of males more than 3.9 mm long; New England, southern Canada to eastern Washington, south to Virginia, New Mexico and Chihuahua (Map 2). ..... *borealis*

Larinia directa (Hentz)

Frontispiece, Plate 1; Figures 1–12, 31, 34, 37–41; Map 1

Epeira directa Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 478, pl. 31, fig. 21, ♀. Type specimens from South Carolina and Alabama destroyed.

Epeira rubella Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 478, pl. 31, fig. 22, ♀. Type specimens from Alabama destroyed.

Epeira tetragnathoides O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 16, pl. 7, figs. 9–10, ♀ ♂. Female, male syntypes from Guatemala and Panama in the British Museum, Natural History. Name preoccupied by *E. tetragnathoides* Walckenaer.

Epeira intercisa O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 18, pl. 5, fig. 11, ♂. Male holotype from Bugaba, Panama in the British Museum, Natural History, lost.

Drexelia directa, – McCook, 1892, Proc. Acad. Natur. Sci. Philadelphia, 127. McCook, 1893, American Spiders, 3: 249, pl. 6, figs. 10, 11, pl. 22, fig. 3, ♀. F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 461, pl.

43, figs. 12, 13, ♀, ♂. Roewer, 1942, Katalog der Araneae, 1: 764. Bonnet, 1956, Bibliographia Araneorum, 2: 1609. Grasshoff, 1971, Senckenbergiana Biol., 52: 93, fig. 45, ♀.

Epeira deludens Keyserling, 1893, Spinnen Amerikas, 4: 261, pl. 13, fig. 195, ♀, ♂. Male and female syntypes from Florida and Guatemala (Marx collection) in the U.S. National Museum, examined.

Larinia bellona Banks, 1898, Proc. California Acad. Sci., ser. 3, 1(7): 257, pl. 15, fig. 6, ♀, ♂. Female, male syntypes from Tepic, Mexico in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Larinia directa, – Emerton, 1902, Common Spiders, p. 182, figs. 424–427, ♀, ♂. Comstock, 1912, Spider Book, p. 508, fig. 545, ♀. Comstock, 1940, Spider Book, rev. ed., p. 521, fig. 545, ♀.

Larinia cymotypa Chamberlin, 1924, Proc. California Acad. Sci., 12: 649, fig. 93. Female holotype from Gulf of California in the California Academy of Sciences, examined. NEW SYNONYMY.

Larinia albonigra Franganillo, 1934, Mem. Soc. Cubana Hist. Natur., 8: 158. Male holotype from Cuba in Cuban Academy of Science, Havana, but with code number only, and no key to code. Franganillo, 1936, Los Arácnidos de Cuba, 81, fig. 38, ♂. NEW SYNONYMY.

Drexelia octopunctata di Caporiacco, 1955, Acta Biol. Venezuelica, 1: 349. Female holotype from Caracas in the Museo de Biol. Universidad Central, Caracas, examined. NEW SYNONYMY.

Larinia nigrovittata Mello-Leitão, 1947, Bol. Mus. Nac., Rio de Janeiro, 80: 12, figs. 26, 27, ♂. Male holotype from Garmo do Rio Claro, Minas Gerais, Brazil in the Museu Nacional, Rio de Janeiro, examined. NEW SYNONYMY.

Note. The Franganillo illustration, made from a squashed palpus on a microscope slide, matches a palpus similarly deformed accidentally. This species is common in Cuba.

Description. Female from Alabama: sternum gray around margin. Dorsum of abdomen with a light median longitudinal band bordered by indistinct darker bands. Total length 11.5 mm. Carapace 3.7 mm long, 2.4 mm wide. First femur, 4.3 mm; patella and tibia, 6.6 mm; metatarsus, 5.5 mm; tarsus, 1.8 mm. Second patella and tibia, 6.0 mm; third, 2.9 mm; fourth, 5.1 mm.

Male from Alabama: color like that of female. Total length 7.5 mm. Carapace 3.4 mm long, 2.2 mm wide. First femur, 4.8 mm; patella and tibia, 7.2 mm; metatarsus, 6.5 mm; tarsus, 2.0 mm. Second patella and tibia, 6.4 mm; third, 2.9 mm; fourth, 5.1 mm.

Variation. Total length of females, 4.8 to 11.7 mm; carapace 1.9 to 3.7 mm long, 1.5 to 2.4 mm wide; first patella and tibia 3.7 to 7.3 mm long. First patella-tibia 1.6 to 2.2 times the length of the carapace. Abdomen length two to three times its width. Total length of males varies 4.5 to 6.5 mm, carapace 1.9 to 2.9 mm long, 1.3 to 1.9 mm wide; first patella and tibia 4.1 to 6.5 mm long. First patella-tibia 2.0 to 2.4 times carapace length.

The size does not vary geographically; the leg length does not vary geographically or with absolute size. Very large individuals were found throughout the range of the species.

The color and markings of the abdomen are variable: there may be a median longitudinal band (Fig. 5) and there may be paired black spots, or these may be absent. There may be black spots on some leg articles. The shape of the abdomen varies greatly but no measurements were made.

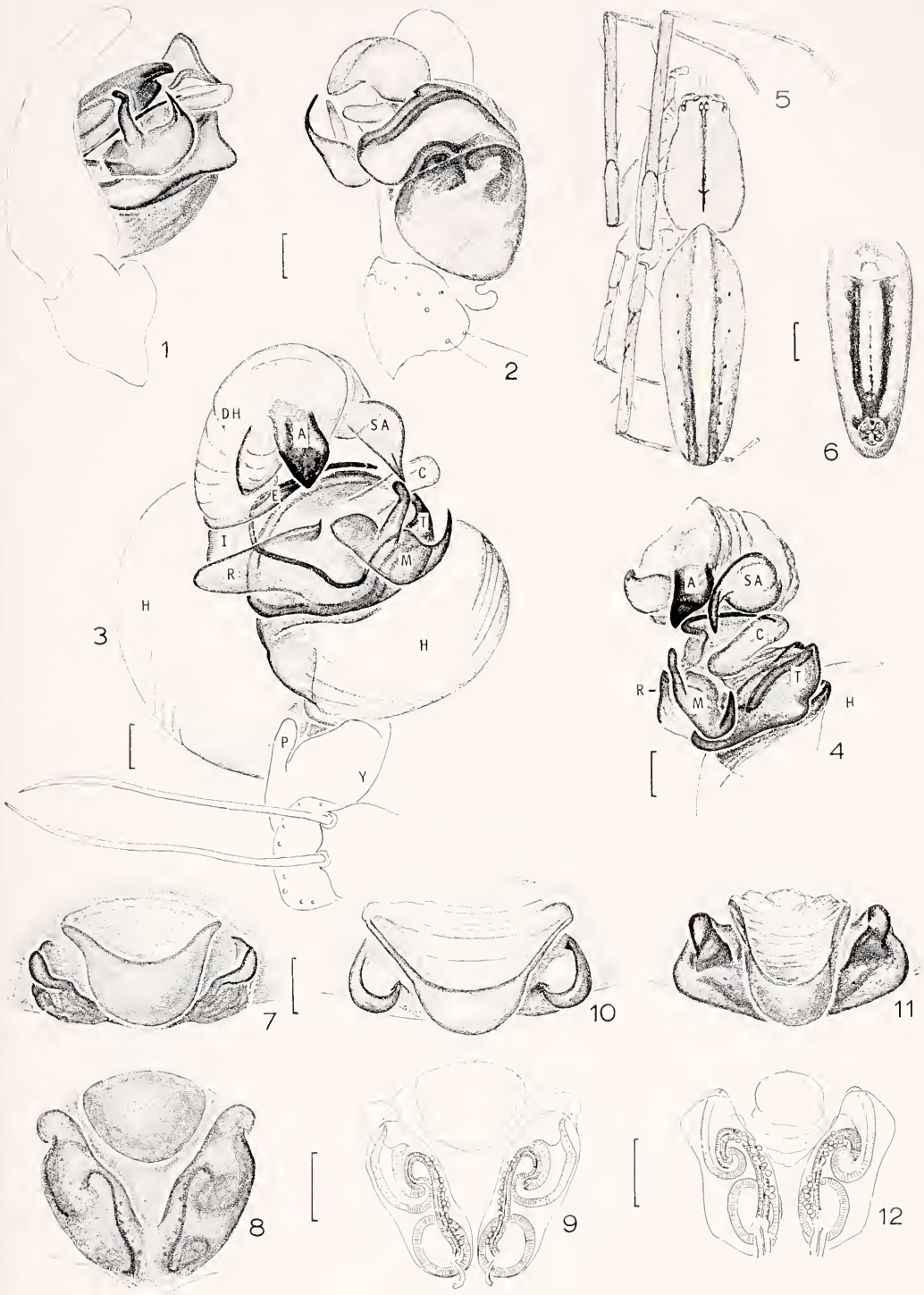
The genitalia are as variable as the size and coloration. The scape may be narrower than long or wider than long, and there is comparable variation in the proportions of the median apophysis.

→

Figures 1–12. *Larinia directa* (Hentz). 1–4. Left male palpus; 1. Mesal, 2. Ventral, 3, 4. Expanded, 3. Bulb, mesal view, 4. Bulb, ventral view. 5, 6. Female; 5. Dorsal, 6. Abdomen, ventral. 7–12. Epigynum; 7, 10, 11. Ventral, 8, 9, 12. Posterior, 9, 12. Cleared. 7–9: (Alabama). 10: (California). 11, 12: (Florida).

Abbreviations. A, terminal apophysis; C, conductor; DH, distal hematodocha; E, embolus; H, basal hematodocha; I, stipes; M, median apophysis; P, paracymbium; R, radix; SA, subterminal apophysis; T, tegulum; Y, cymbium.

Size indicators: 0.1 mm, except Figures 5, 6, 1.0 mm.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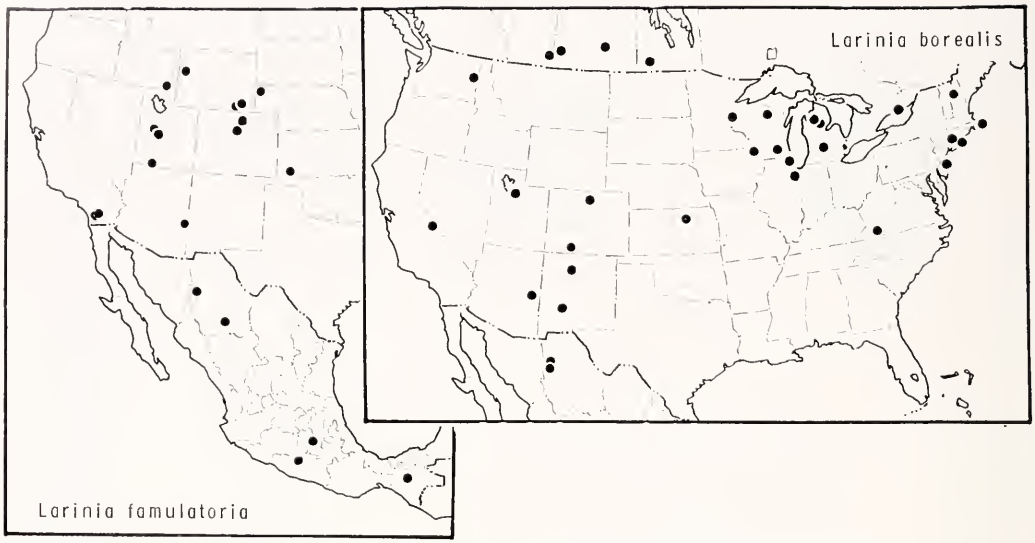


Map 2. Distributions of *Larinia borealis* Banks and *L. famulatoria* (Keyserling).

Diagnosis. Both males and females have much longer legs than do other species. The first patella-tibia of the female is 1.6 to 2.2 times carapace length (Fig. 5), of the male 2.0 to 2.4 mm. The scape of the epigynum has an unusual, wide rim distally (Figs. 7, 10, 11). The embolus is flatter than that of other species (Figs. 1, 34).

Natural History. Larinia directa females are mature throughout the season and adult males have been collected from March to September. The oblique web is found in grass and on herbs (Comstock, 1940). Very few specimens have data on habits: it has been collected in grass in Louisiana, an old field in North Carolina, a cotton field in Arkansas, a pine forest in Chiapas and a banana plantation in Panama. In Cali, Colombia specimens are found in weedy fields and the web is made in the evening (Frontispiece and W. Eberhard, personal communication).

Distribution. From Lakehurst, New Jersey (J. and W. Ivie), 27 June 1964, to southern California, south to Brazil (Map 1).

Larinia borealis Banks
Figures 13–21, 32, 35, 42–44; Map 2

Larinia borealis Banks, 1894, Entomol. News, 5: 8. One female, two juvenile syntypes from Franconia, New Hampshire in the Museum of Comparative Zoology, examined. McCook, 1894, American Spiders, 3: 247, pl. 22, figs. 1, 2, ♀, ♂. Comstock, 1912, Spider Book, p. 508, Comstock, 1940, Spider Book, rev. ed., p. 521. Roewer, 1942, Katalog der Araneae, 1: 772. Kaston, 1947, Connecticut Geol. Nat. Hist. Surv., 70: 228, figs. 732–733, ♀. Bonnet, 1957, Bibliographia Araneorum, 2(3): 2348.

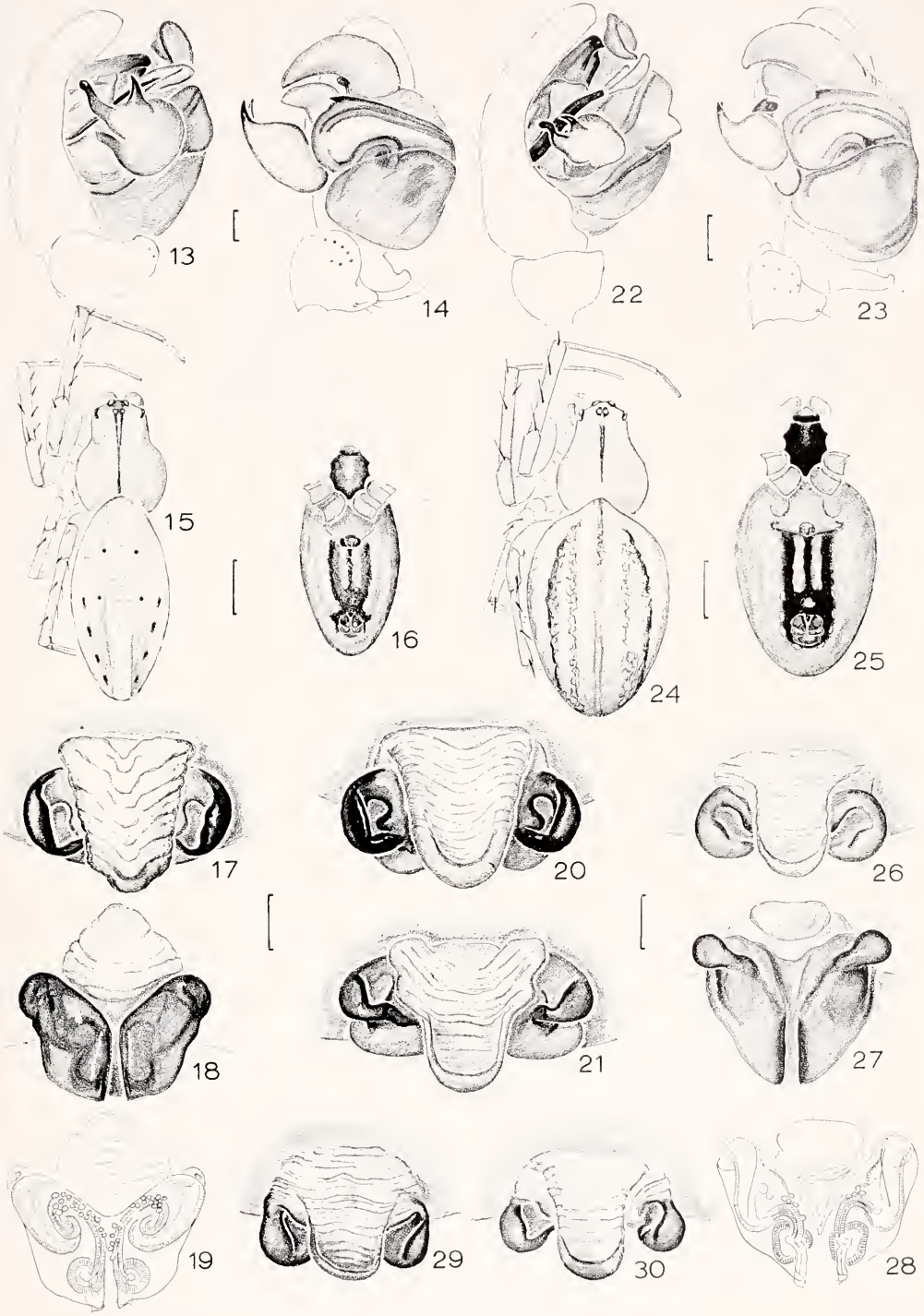
Drexelia borealis, – Grasshoff, 1971, Senckenbergiana Biol., 52: 89, fig. 40, ♀, ♂.

→

Figures 13–21. *Larinia borealis* Banks. 13, 14. Left palpus; 13, Mesal. 14. Ventral. 15, 16. Female; 15. Dorsal, 16. Abdomen ventral. 17–21. Epigynum; 17, 20, 21. Ventral, 18, 19. Posterior, 19. Cleared. 17–18: (New Hampshire). 19: (Alberta). 20: (Saskatchewan). 21: (Utah).

Figures 22–30. *Larinia famulatoria* (Keyserling). 22, 23. Palpus; 22. Mesal, 23. Ventral. 24, 25. Female; 24. Dorsal, 25. Abdomen, ventral. 26–30. Epigynum; 26, 29, 30. Ventral, 27, 28. Posterior, 28. Cleared. 26–28: (Idaho). 29: (Colorado). 30: (Utah).

Size indicators: 0.1 mm, except Figures 15, 16, 24, 25, 1.0 mm.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Description. Female syntype: proximal part of labium and endites dark brown. Sternum dark brown. Dorsum of abdomen with a median dorsal light band and four pairs of small black streaks posteriorly (Fig. 15). Venter between epigynum and spinnerets dark, enclosing two white longitudinal streaks (Fig. 16). Total length 5.3 mm. Carapace 2.1 mm long, 1.5 mm wide. First femur, 2.1 mm; patella and tibia, 2.7 mm; metatarsus, 1.9 mm; tarsus, 0.8 mm. Second patella and tibia, 2.4 mm; third, 1.4 mm; fourth, 2.3 mm.

Description of male from Manitoba: total length 5.4 mm. Carapace 2.6 mm long, 1.9 mm wide. First femur, 2.7 mm; patella and tibia, 3.5 mm; metatarsus, 2.7 mm; tarsus, 1.0 mm. Second patella and tibia, 3.0 mm; third, 1.7 mm; fourth, 3.0 mm.

Variation. The abdominal coloration is as variable as that of *Larinia directa*. Rarely are there paired, median dorsal black marks. Females varied from 4.5 to 8.0 mm in total length, carapace 1.7 to 3.0 mm long, 1.4 to 2.3 mm wide; first patella and tibia, 2.3 to 4.3 mm long; ratio of first patella and tibia length to carapace 1.2 to 1.6. The length of the abdomen is about twice its width. Males 3.9 to 5.4 mm in total length, carapace 1.7 to 2.5 mm long, 1.3 to 1.9 mm wide; first patella and tibia, 2.9 to 3.5 mm long; ratio of first patella and tibia to carapace 1.4 to 1.7.

Diagnosis. The epigynum of *L. borealis* differs from that of *L. directa* by the narrow posterior rim of the scape and by the medially, posteriorly directed basal wrinkles on the scape (Figs. 17, 20, 21) from *L. famulatoria*. It differs from both species in that the lip of the opening in ventral view makes a right angle, bordering the depression both laterally and posteriorly (Figs. 17, 20, 21). The male differs from *L. directa* by having shorter legs and from *L. famulatoria* having less distinct markings ventrally. Unlike the lobed embolus of *L. famulatoria*, the embolus of *L. borealis* tapers to its tip (Figs. 13, 35).

Natural History. Larinia borealis has been collected by sweeping an old field and in a pine forest in Michigan, from dry limy prairie, by sweeping herbs, from tall grasses, from a sandy area in Wisconsin, and by sweeping pines in Illinois. Adult males have been collected from May to October.

Distribution. New England, southern Canada to eastern Washington south to Virginia, Kansas and Chihuahua (Map 2).

Larinia famulatoria (Keyserling)
Figures 22–30, 33, 36, 45, 46; Map 2

Epeira famulatoria Keyserling, 1883, Verhandl. Zool. Bot. Gesell. Wien, 32: 201, pl. 15, fig. 6, ♀. Female holotype from Colorado in the Naturhistorisches Museum, Vienna, lost. Female neotype here designated from Fort Collins, Colorado, in the Museum of Comparative Zoology. Keyserling, 1893, Spinnen Amerikas, 4: 231, pl. 11, fig. 172, ♀.

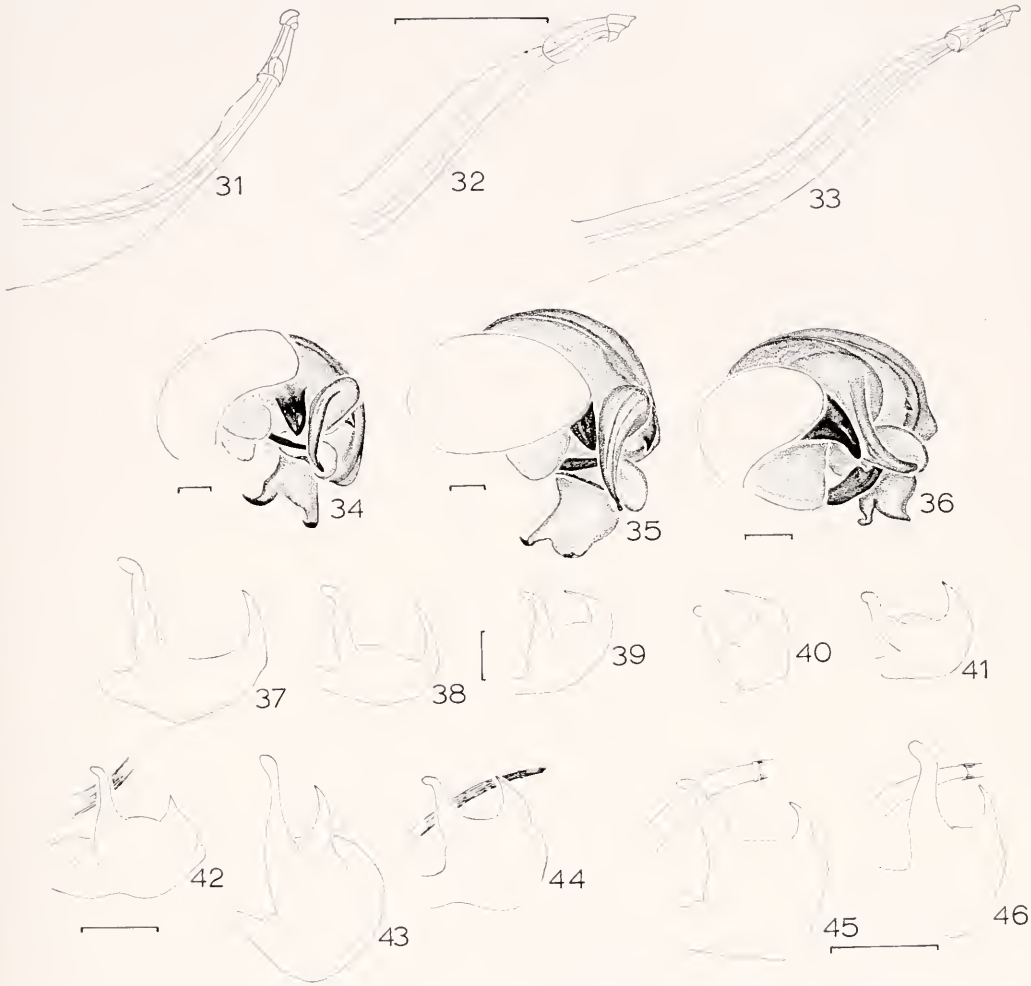
Epeira mormon Keyserling, 1892, Spinnen Amerikas, 4: 182, pl. 9, fig. 134, ♀. Two female syntypes from "District of Columbia" Marx collection (type locality in error) in the U. S. National Museum, examined. Keyserling reports as type specimens one from Utah, one from District of Columbia. McCook, 1893, American Spiders, 3: 164, pl. 6, fig. 5, ♀. NEW SYNONYMY.

Aranea mormon, – F. O. P.-Cambridge, 1904, Biologia Centrali-Americana, 2: 517, pl. 51, fig. 1, ♀. Roewer, 1942, Katalog der Araneae, 1: 861.

Larinia famulatoria, – Comstock, 1912, Spider Book, p. 509; Comstock, 1940, Spider Book, rev. ed., p. 522. Roewer, 1942, Katalog der Araneae, 1: 772. Bonnet, 1957, Bibliographia Araneorum, 2: 2349.

Araneus mormon, – Bonnet, 1955, Bibliographia Araneorum, 2: 546.

Description. Female from Idaho: labium posteriorly black, sternum black. Legs often with a line of black dots on venter of femora (Fig. 25). Dorsum of abdomen with indistinct longitudinal bands, the lateral ones having dark lateral borders (Fig. 24). Venter black between epigynum and around spinnerets, enclosing a longitudinal white band, which is broken in the center by a black line (Fig. 25). Total length 5.4 mm. Carapace 2.2 mm long, 1.5 mm wide. First femur, 1.8 mm; patella and tibia, 2.4 mm; metatarsus, 1.9 mm; tarsus,



Figures 31–33. *Larinia* left virgin embolus with cap; 31. *L. directa*, 32. *L. borealis*, 33. *L. famulatoria*. Figures 34–36. *Larina* left palpus in apical view; 34. *L. directa*, 35. *L. borealis*, 36. *L. famulatoria*. Figures 37–46. *Larinia*, median apophysis of left palpus; 37–41. *L. directa*; 37: (North Carolina). 38, 39: (Florida). 40: (Jamaica). 41: (Colombia). 42–44. *L. borealis*; 42: (Michigan). 43: (Saskatchewan). 44: (Massachusetts). 45, 46: *L. famulatoria*, (Utah).

Size indicators: 0.1 mm.

0.8 mm. Second patella and tibia, 2.2 mm; third, 1.4 mm; fourth, 2.2 mm.

Male: total length 3.5 mm. Carapace 1.7 mm long, 1.3 mm wide. First femur, 1.9 mm; patella and tibia, 2.2 mm; metatarsus, 1.9 mm; tarsus, 0.7 mm. Second patella and tibia, 2.1 mm; third, 1.2 mm; fourth, 1.9 mm.

Variation. Unlike *Larinia directa* and *L. borealis*, *L. famulatoria* has the dorsal abdominal pattern alike in all well-preserved specimens. Females varied from 3.2 to 5.6 mm total length, 1.4 to 2.1 mm carapace length, 1.2 to 1.4 mm carapace width and first patella and tibia 1.7 to 2.6 mm. Males varied from 2.9 to 3.3 mm total length, carapace 1.4 to 1.7 mm long, 1.1 to 1.2 mm wide, first patella and tibia 2.0 to 2.3 mm. The ratio of first patella and tibia to carapace length varied 1.1 to 1.3 in females,

1.4 to 1.5 in males. The length of the abdomen is about 1.2 to 1.5 times its width.

Diagnosis. Females and males can be separated from those of *L. directa* by the much shorter first patella and tibia (Fig. 24). *Larinia famulatoria* differs from *L. borealis* by the wider, shorter abdomen (Fig. 24), the ventral pattern (Fig. 25) and the genitalia. Females have the sides of the scape almost parallel, with the basal striations transverse (Figs. 26, 29, 30), while the scape of *L. borealis* tapers to the tip and the chevron-shaped basal striations point toward the tip. The males of *L. famulatoria* are shorter in total length than males of *L. borealis*. In the male of *L. famulatoria*, the embolus is thicker and wider than the prongs of the median apophysis (Fig. 22); in lateral view the embolus is much narrower in *L. borealis* and *L. directa* when viewed from the side. The tip of the embolus below the cap has a lobe that is easily seen in apical view (Fig. 36). The lobe may be transparent, but is not present in other species.

Distribution. Wyoming, Idaho, western Kansas to southern California and to southern Mexico (Map 2).

Cercidia Thorell

Cerceis Menge, 1866, Schrift. Naturf. Gesell. Danzig, neue Folge, 1: 80. Type species by monotypy: *Cerceis prominens* (Westring). Name is preoccupied by *Cerceis* Rafinesque, 1815, a polychaete, *Cerceis* Milne Edwards, 1840, a crustacean, and *Cerceis* Gistl, 1848, a mollusk.

Cercidia Thorell, 1869, On European Spiders, p. 58. Type species designated by Thorell, 1869 and by monotypy *Epeira prominens* Westring. The generic name is of feminine gender.

Description. The eyes are relatively closely spaced, as in small species of *Araneus*. The abdomen is oval, widest in the middle and slightly pointed anteriorly (Fig. 53). The legs are short, the fourth longest with very few macrosetae.

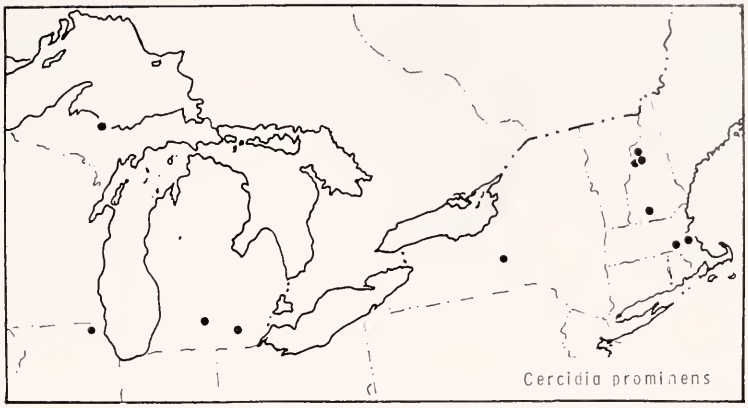
The genitalia of both sexes are heavily sclerotized. The epigynum has a scape bearing setae (Fig. 55). The internal genitalia are heavily sclerotized and complex (Fig. 57).

The male palpus (Figs. 47–49) is like that of small species of *Araneus*. As far as can be determined it lacks the embolus cap. The embolus tip is hidden below the terminal apophysis and behind the conductor. There are two macrosetae on the palpal patella. Males are slightly smaller than females, have a slightly longer and more sclerotized scutum on the abdomen. The first coxa has a distal, retrolateral hook which fits into a groove of the second femur. The second tibia is modified by bearing macrosetae on its anterior surface.

The genitalia of *Cercidia prominens* are surprisingly similar to that of *Araneus pratensis* (Emerton) (Levi, 1973, Bull. Mus. Comp. Zool. 145 (9), figs. 21–31) and I think that *C. prominens* is closely related to this species. But *C. prominens* differs by being more sclerotized, having a high clypeus and having fourth leg longer than first.

Diagnosis. Cercidia can be separated from *Araneus* and other araneid genera by the oval, anteriorly slightly-pointed abdomen, and the dorsal abdominal scutum, with its line of short, dark macrosetae around the anterior end. The height of the clypeus is 2.5 times the diameter of the anterior median eyes, while in most related Araneidae, the clypeus is about equal to the eye diameter. The fourth legs are slightly longer than the first.

Note. Sclerotization is commonly found in very small spiders that live in the soil, an adaptation to increased surface per volume, presumably protecting against water loss. Sclerotization is found also in those araneids which stay in the center of the web at midday, exposed to sunlight (e.g., *Gasteracantha*, *Micrathena*). The high clypeus perhaps is correlated with sclerotization, but it is not found in *Gasteracantha* or *Micrathena*. *Cercidia prominens* makes its small webs above the ground, often in open areas. *Pronous*, the only araneid I know to practice a similar habit, is not



Map 3. Distribution of *Cercidia prominens* (Westring) in North America.

sclerotized, but *Pronous* is found in moist tropical forests in Central and South America.

Micrathena has the fourth legs longer than the first, presumably to permit its peculiar resting position in the center of the vertical web, with the abdomen held horizontal, dorsum parallel to the ground. I do not know the significance of long fourth leg in *Cercidia,* but I do not know its resting position.

Cercidia prominens is the only species definitely belonging to the genus. It is probably European in origin, having been accidentally introduced to the northeastern states of North America.

Misplaced species. Simon (1889, J. Asiatic Soc. Bengal, 58, Suppl., p. 382) described males and females of *C. punctigera* from Bengal. Its placement is unknown. I doubt that it belongs to *Cercidia.* It has never been illustrated.

Archer (1951a) placed *Epeira albostriata* Keyserling of South America in *Cercidia.* But this species belongs in the genus called *Lariniacantha* by Archer (1951a). *Epeira albostriata* is the type species of the Mello-Leitão (1933) genus *Parepeira,* and is close to what O. P.-Cambridge (1889) called *Alpaida.* The species is not close to *Cercidia* at all.

Cercidia funebris Keyserling, 1892, Spinnen Amerikas, 4: 37, pl. 2, fig. 32, ♀. Female holotype from Crescent City, Florida (locality doubtful, as the specimen is from the Marx collection) belonging to the U. S. National Museum, but kept in the American Museum of Natural History, was examined and is *Hypsosinga singaeformis* (Scheffer, 1903), NEW SYNONYMY. The Keyserling name is older, and as the Scheffer name has been used less than ten times, it will have to be placed in synonymy with *Hypsosinga funebris* (Keyserling, 1892), NEW COMBINATION.

Cercidia octomaculata Mello-Leitão, 1945, Rev. Mus. La Plata, 4: 236, fig. 10, ♀. Female holotype from Pindapoy, Misiones, Argentina in the La Plata Museum, examined. It belongs to the genus *Alpaida.*

Cercidia prominens (Westring)
Figures 47–57; Map 3

Epeira prominens Westring, 1851, Göteborg Kongl. Vetenskap Handl., 2: 35. Male type from Sweden. In the dry Westring Collection of the Swedish Museum of Natural History, Stockholm, there are two specimens, male and female.

Epeira bella Meade, 1861, Ann. Mag. Natur. Hist., ser. 3, 7: 20. Male and female holotypes from near Bicester, Oxfordshire, England, depository unknown.

Singa scutifera Westring, 1861, Araneae Svecicae, p. 66. Female holotype from Sweden. In the dry collection of Westring in the Swedish Museum of Natural History there are some specimens, probably labeled by Thorell.

Atea spinosa Oblert, 1865, Programm Realschule Königsberg, 9 (publication unavailable).

Cercis prominens, – Menge, 1866, Schrift. Naturf. Gesell. Danzig, neue Folge, 1: 80, pl. 13, fig. 21 ♀, ♂.

Miranda carinata Giebel, 1869, Z. gesammt. Naturwiss. 34: 301. Female holotype from Vierwaldstädter See, Switzerland in the University Museum Halle, not examined.

Cercidia prominens, – Thorell, 1869, On European Spiders, p. 49, 58. Comstock, 1912, Spider Book p. 455. Emerton, 1913, Trans. Connecticut Acad. Sci., 18: 219, pl. 2, fig. 11, ♀. Wiehle, 1931, in Dahl, Tierwelt Deutschlands, 23: 25, figs. 10, 30–32, ♀, ♂. Comstock, 1940, Spider Book, rev. ed., p. 469. Roewer, 1942, Katalog der Araneae, 1: 865. Kaston, 1948, Connecticut Geol. Natur. Hist. Surv., 70: 227, fig. 731, ♀. Archer, 1951, Am. Mus. Novitates, no. 1487: 42. Locket and Millidge, 1953, British Spiders, 2: 159, fig. 106, ♀, ♂.

Araneus prominens, – Bonnet, 1955, Bibliographia Araneorum, 2: 568.

Description. Female from England: specimens in alcohol have carapace orange-brown with a dark thoracic spot. Sternum dark brown, legs orange-brown, dorsum of abdomen orange-brown with a median longitudinal light band indistinctly bordered and four dark spots on the anterior of scutum. Under the scutum is a reticulate pattern (Fig. 53). Sides of abdomen orange; venter very dark between epigynum and spinnerets, and on sides of dark area is a white pigment band, which grades into the darker sides. Eyes subequal in size. Anterior median eyes slightly more than their diameter apart, slightly more than their diameter from laterals. Posterior median eyes their diameter apart, slightly less than two from laterals. Chelicerae heavy, with four teeth on anterior margin, two or three on posterior. Total length 5.4 mm. Carapace 2.2 mm long, 1.6 mm wide. First patella and tibia, 1.7 mm; second, 1.5 mm; third, 1.1 mm. Fourth femur, 1.6 mm; patella and tibia, 1.9 mm; metatarsus, 1.1 mm; tarsus, 0.7 mm.

Male: coloration like that of female, but sclerotized parts, including the carapace darker. Thoracic area with very slight depression with a dark spot. Eye sizes as in female, slightly farther apart. Clypeus as in female. Abdomen with a dorsal shield, lightly sclerotized, which covers three-quarters of abdomen. Total length 3.9 mm. Carapace 2.0 mm long, 1.7 mm wide. First patella and tibia, 1.7 mm; second, 1.5 mm; third, 1.1 mm. Fourth femur, 1.4 mm; patella and tibia, 1.7 mm; metatarsus, 0.9 mm; tarsus, 0.7 mm.

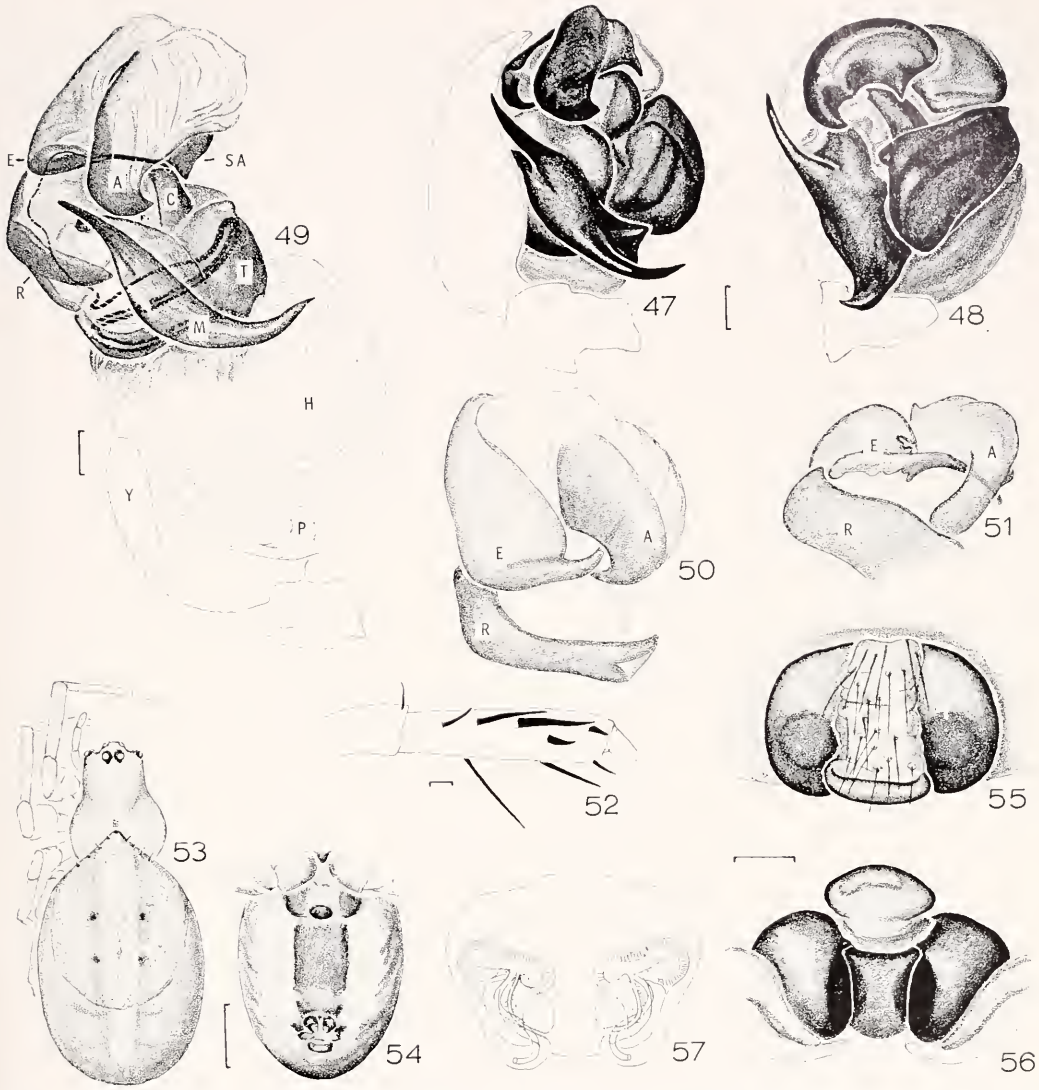
Variation. Females collected in North America varied from 3.8 to 4.6 mm in total length, carapace 1.7 to 2.1 mm long, 1.4 to 1.6 mm wide. Males varied from 3.6 to 4.1 mm in total length, carapace 1.7 to 1.9 mm long, 1.4 to 1.6 mm wide.

Note. The color of living specimens is orange-red. The illustrations were made from specimens collected in England.

Natural History. Adult males have been collected in May, July and November in North America; adult females from May to November. The only one I ever found was hanging on a thread in a low bush in the relatively open vegetation of the top of North Pack Monadnock Mountain in New Hampshire. Unfortunately, I placed it in alcohol, thinking it was an unusually colored specimen of *Araniella displicata*. Other specimens came from "sifting" and a tamarack bog.

According to Wiehle (1931), *Cercidia prominens* is found below 300 m elevation in Central European mountains, the hub of the web is 4 to 6 cm above the ground, and the web is between grasses, low plants, mosses or litter and may be in open areas as well as in forest. Wiehle found it difficult to collect *C. prominens* except by searching carefully above the ground or by sifting litter.

The web is made in the afternoon and removed late in the morning, even though not damaged. The orb has between 12 and 21 radii and the diameter of the viscid thread area is 50 to 60 mm. The center is open and there are 18 viscid turns above the hub, 27 below, both crossing radii for about 19 mm distance, the threads below being spaced closer than those above. The spider rests in the center and there is no retreat. If disturbed the spider shakes the



Figures 47–57. *Cercidia prominens* (Westring). Figures 47–51. Left palpus; 47. Mesal, 48. Ventral, 49–51. Expanded; 49. Bulb in submesal view, 50. Apical view, 51. Radix and embolus viewed from below. 52. Left second tibia, prolateral. 53, 54. Female; 53. Dorsal view, 54. Ventral. 55–57. Epigynum; 55. Ventral, 56. Posterior, 57. Dorsal, cleared.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; H, basal hematodocha; M, median apophysis; P, paracymbium; R, radix; T, tegulum; Y, cymbium.

Size indicators: 0.1 mm, except Figures 53, 54, 1.0 mm.

web before dropping and disappearing in the ground litter. Males and females are mature until fall (Wiehle, 1931).

The spherical egg sac is of orange curled threads, somewhat similar to that of *Ero* without a stalk, and contains 15 orange, relatively large, eggs. The eggs overwinter in litter (Menge, 1866).

Individuals just leaving the egg sac have three black spots on the posterior end of the dorsal side of the abdomen (Wiehle, 1931).

Distribution. Michigan, New Hampshire and Massachusetts (Map 3). Although difficult to collect (Wiehle, 1931), this spider is so conspicuous that its spotty distribution is puzzling. Its occurrence in the Lake States and New England suggests that the species has been introduced. But one would not expect an introduced species to be found in the Moosilauke region and on North Pack Monadnock Mountain in New Hampshire. West Quincy, (where the species was first collected in 1877) and Holliston, Massachusetts, and Marquette, Michigan are localities more characteristic of an introduced animal.

Records. Massachusetts. Norfolk Co.: West Quincy, 15 Nov. 1877, ♀ (J. H. Emerton). Middlesex Co.: Holliston, 2 May 1926, ♀ (E. B. Bryant); May, June-July, Sept., Nov. 1923, ♀♂ (J. H. Emerton). *New Hampshire.* Grafton Co.: Moosilauke, 4 July 1912, ♂ (E. B. Bryant); North Woodstock, Sept. 1911, ♀ (W. Fox); Franconia, ♀♂ (N. Banks). Hillsboro Co.: North Pack Monadnock Mtn., Oct. 1972, ♀ (H. W. Levi). *New York.* Tompkins Co.: McLean, 29 May 1937, ♂ (Gerberg, Greenspan). *Michigan.* Lenawee Co.: Burke Lake, Clinton, swept, 22 May 1970, ♂ (N. Platnick). Marquette Co.: Marquette, 26, 29 July 1932, ♀♂ (A. M. Chickering); Calhoun Co.: Marshall, tamarack swamp, 11 May 1935, ♀ (A. M. Chickering). *Illinois.* Lake Co.: Volo bog, 27 April 1935, 2 ♀ (D. C. Lowrie).

There are also specimens from England, Germany, Denmark, Poland, Switzerland and France in American collections.

Mangora O.P.-Cambridge

Mangora O. P.-Cambridge, 1889, Biologia Centrali-Americana, 1: 13. The type species is *Mangora picta* O. P.-Cambridge from Guatemala, designated by Simon, 1895, Histoire Naturelle des Araignées, 1: 793. The generic name is feminine.

Abbotia McCook, 1894, American Spiders, 3: 239. Type species *Mangora gibberosa* (Hentz), designated by F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 477. The generic name is preoccupied by Leach, 1830 for a Coleopteran.

Prasonica Simon, 1895, Histoire Naturelle des Araignées, 1: 794. The type species is *P. albolimbata* Simon, 1895 from Madagascar by original designation. The type specimen is a juvenile in the Muséum National d'Histoire Naturelle, examined. NEW SYNONYMY.*

Psyllo Thorell, 1899, Bihang. Kongl. Svenska Vetenskap. Akad. Handl., 25: 39. The type species is *Psyllo nitida* Thorell, 1899 from Cameroon by monotypy. Female holotype in the Stockholm Natural History Museum, examined. NEW SYNONYMY.*

Abbotiana Strand, 1929, Acta Univ. Latviensis, 20: 10. New name for *Abbotia* McCook, a preoccupied name.

Description. The carapace is pear-shaped, highest in the thoracic region, and quite narrow in the eye region (Fig. 58). The height of the clypeus is less than the diameter of the anterior median eyes. The abdomen is ovoid, widest in the middle or in the posterior half and held at an angle of about 135° (Fig. 59). The legs are of intermediate length with many long macrosetae (Figs. 59, 118). The coloration and marks are diagnostic for many species.

The anterior median eyes may be slightly larger than the posterior medians, sometimes subequal, but in *M. calcarifera* they are a little smaller. The lateral eyes are between 0.7 and 0.9 diameters of the anterior median eyes in size.

The anterior median eyes are always separated by about their diameter and the same distance or slightly more from the anterior laterals, at most 1.5 diameters from the laterals in *M. maculata*, 1.4 in *M. passiva*. The posterior median eyes are also separated by about their diameter or slightly less, and by their diameter or two diameters at most from the posterior laterals. The secondary eyes have black rings and the posterior medians often have wide black rings.

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* Grasshoff (personal communication) considers these genera, as well as his own *Prasonicella* and *Umbonata*, distinct because of the carapace shape and different arrangement of the feathered trichobothria on the third tibia. Grasshoff may be right and I may find it desirable to separate these genera when I study the neotropical *Mangora*.

Genitalia. The female epigynum may have a scape (Fig. 61) in temperate species but lacks a scape (Fig. 133) in many tropical American species. The epigynum is very lightly sclerotized in those with a scape. The posterior view of the epigynum and the internal genitalia, the shape of the seminal receptacles and the ducts, are diagnostic features that separate the species.

The male palpus is complex. It has a conductor, a small median apophysis with one or two points (Figs. 68, 80, 127), a complex and sometimes huge embolus (Figs. 68, 127), and a terminal apophysis. The terminal apophysis is on a large hematodocha, and below the terminal apophysis is an odd sclerite which is difficult to homologize but is probably a subterminal apophysis. The palpal patella has only one macroseta. (There are two in *Araneus* and many araneid genera, three in *Araniella.*)

The males are only slightly smaller (1.9 to 4.0 mm) than females (2.3 to 5.5 mm), have the same shape, and similar pattern and eye distances. The first coxa in all species has a hook on the posterior distal margin, and there is a groove on the second femur; the legs are not otherwise modified, except sometimes by strong macrosetae on the second tibia.

Diagnosis. *Mangora* species can be separated from other araneid species by two very distinct characters: the carapace is very high in the thoracic region, sloping down gently toward the head region, more abruptly toward the posterior margin (Figs. 59, 94, 118), and the prolateral surface of the third tibia of both males and females has transverse rows of long, feathered trichobothria (Figs. 59, 64). Also the abdomen is attached to the cephalothorax at a peculiar angle.

Relationships. The type species for the name *Mangora* will be illustrated in the planned revision of the tropical American species. It is similar to *M. calcarifera* but has a short embolus supported by the conductor and short epigynal ducts. It is less specialized than *M. calcarifera.* Palpal structure (Figs. 102–109) and function of the only European species, *Mangora acalypha,* have been studied in detail by Grasshoff (1973). Grasshoff indicated that the *Mangora* palpus lacks a conductor; but I believe Grasshoff's "Teg F" is the missing structure. The structure I consider the subterminal apophysis was called subterminal apophysis 1 by Grasshoff. The subterminal apophysis 2 of Grasshoff, I consider to be a part of the terminal apophysis (judging by the examination of the structure in a number of species).

There appear to be two species groups in America, the *M. acalypha* group with a scape in the epigynum, and the *M. picta* group without a scape (Figs. 131, 133). The *M. picta* group is better represented in tropical America but has only one species, *M. calcarifera,* that extends into the area under consideration here. *Mangora acalypha,* of the first group, has been studied in detail by Grasshoff, not only the structure but also the function of the palpus: the spine of the median apophysis hooks into the tip of the scape, as it does in other Araneidae and Linyphiidae examined. The paracymbium in the expanded palpus lies on the median apophysis, preventing it from turning and, in turn, is prevented from moving by the radix, under which it lies. The massive subterminal apophysis lies between tegulum and the base of the epigynum, opposed by the conductor, which presses on the side of the scape.

Mangora calcarifera, representing the *M. picta* group, has a very different palpus. The large subterminal apophysis present in the *M. acalypha* group (Fig. 129) cannot be found (Figs. 143, 144). The median apophysis has changed in position and is located behind what I believe to be the conductor. I believe the conductor to be the structure that grows out of the tegulum at the point at which the sperm duct makes its appearance on the side of the tegulum; coming from the embolus through the inside of the bulb and continuing below the

surface of the tegulum into the subtegulum. In *M. calcarifera,* the conductor is just a lobe. The terminal apophysis, as in the *M. acalypha* group, is a complex sclerite. The filament of the long embolus of *M. calcarifera* is held by the radix, an unusual feature characteristic of the species rather than the species group. The tip of the embolus usually lies against the conductor.

At present I think that the palpus of *M. calcarifera* is derived from a more complex palpus rather than being primitive. The palpus appears to have lost secondarily the subterminal apophysis, judging by the palpal complexity, and the epigynum has secondarily lost the scape. The conductor and median apophysis have lost their function and have (secondarily) become reduced. If the structure were primitively simple I would expect the conductor and median apophysis to be absent.

I have not studied the tropical species carefully. I have made drawings, but have not expanded the palpi to study their structure. But superficial examination indicates that *M. calcarifera* is an extreme form of a very diverse group and there are species intermediate between the *M. acalypha* group and *M. calcarifera.* The epigynal scape also shows intermediate forms, reduction to a fixed inflexible median extension of the base, to total disappearance.

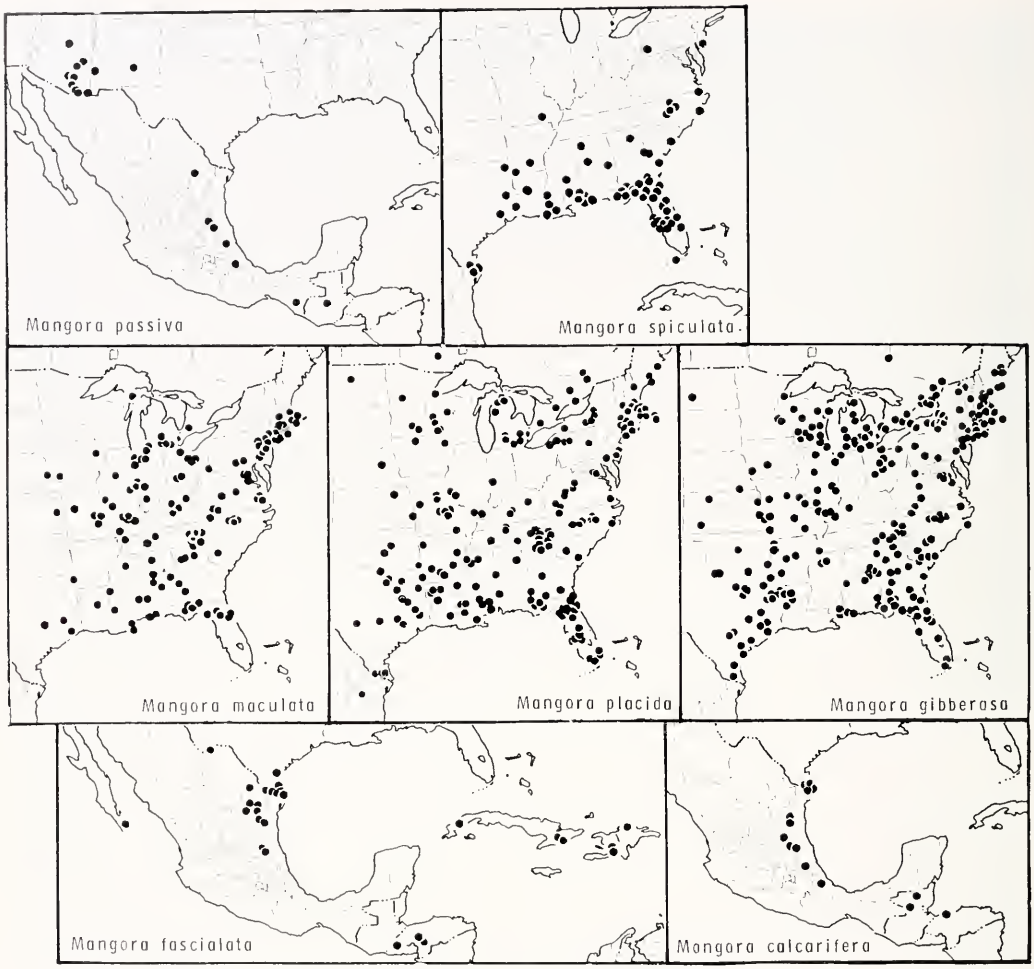
Archer's work on *Mangora* (1951a) is confused and is difficult to follow. Archer, given specimens of a new species by Wilton Ivie, described them as *M. floridana.* But other specimens of this same species from Alabama he labeled correctly as *M. spiculata.* One of these is here designated a neotype of *Epeira spiculata.* However, in his publication (1951a), Archer pictured the species generally considered to be *M. placida* since the time of Emerton (1884, Trans. Connecticut Acad. Sci., 6: 316), called it *spiculata,* and labeled the illustrations of his specimens of *M. spiculata* as *M. placida.* This is a departure from his mostly correct determinations and from all previous usage, and will not be followed here.

Natural History. The most common species in the eastern United States are *M. placida* and *M. maculata,* both common in the undergrowth of woods, *M. maculata* being mature in summer, *M. placida* in spring. *Mangora gibberosa* is more common in fields and meadows and is mature from early to late summer. But forest species may be found in fields and *M. gibberosa* sometimes in woods.

The orb-web of *Mangora* species is vertical to horizontal, very finely meshed and has many closely spaced threads. *Mangora gibberosa* has 50 to 60 radii (Kaston, 1948) and more than 50 viscid threads in the lower half (Plate 2). *Mangora acalypha* of Europe also has 50 to 60 radii and 50 to 60 viscous threads. The hub in the center has 10 to 12 turns and there is a free zone between it and the viscous threads (Wiehle, 1931). Wiehle observed the laying of the scaffolding threads: 10 turns with 510 attachments, finished in seven minutes. The web is probably replaced every morning, judging by its perfect condition in the early hours. There is no retreat. The spider hangs in the hub and when disturbed runs to a grass blade on the side or drops on a thread (Plate 2).

Distribution. Although there is one European species, several species have been described from Africa, and several from eastern Asia; most species are American. Of the perhaps 30 to 50 American species, only seven are found north of Mexico. One of these, *M. passiva,* is found in the southwest to Central America; all others are eastern. Only *M. placida, M. maculata,* and *M. gibberosa* are found in southern Canada, and *M. calcarifera* and *M. fascialata* are found only in southern Texas. The range of *M. calcarifera* extends to Central America, that of *M. fascialata* to Baja California, Central America (Map 4) and the West Indies (Map 4). The many tropical species of *Mangora* are more diverse, some

Plate 2. *Mangora gibberosa*, female, in field in Massachusetts with morning dew.



Map 4. Distribution of the species of *Mangora* occurring north of Mexico.

smaller, others larger, than the few species of the temperate region.

KEY TO SPECIES OF *MANGORA* NORTH OF MEXICO

1 A black longitudinal line on venters of femora one and two (Fig. 118); dorsum of abdomen with 2–3 lines (Figs. 110, 119). 2

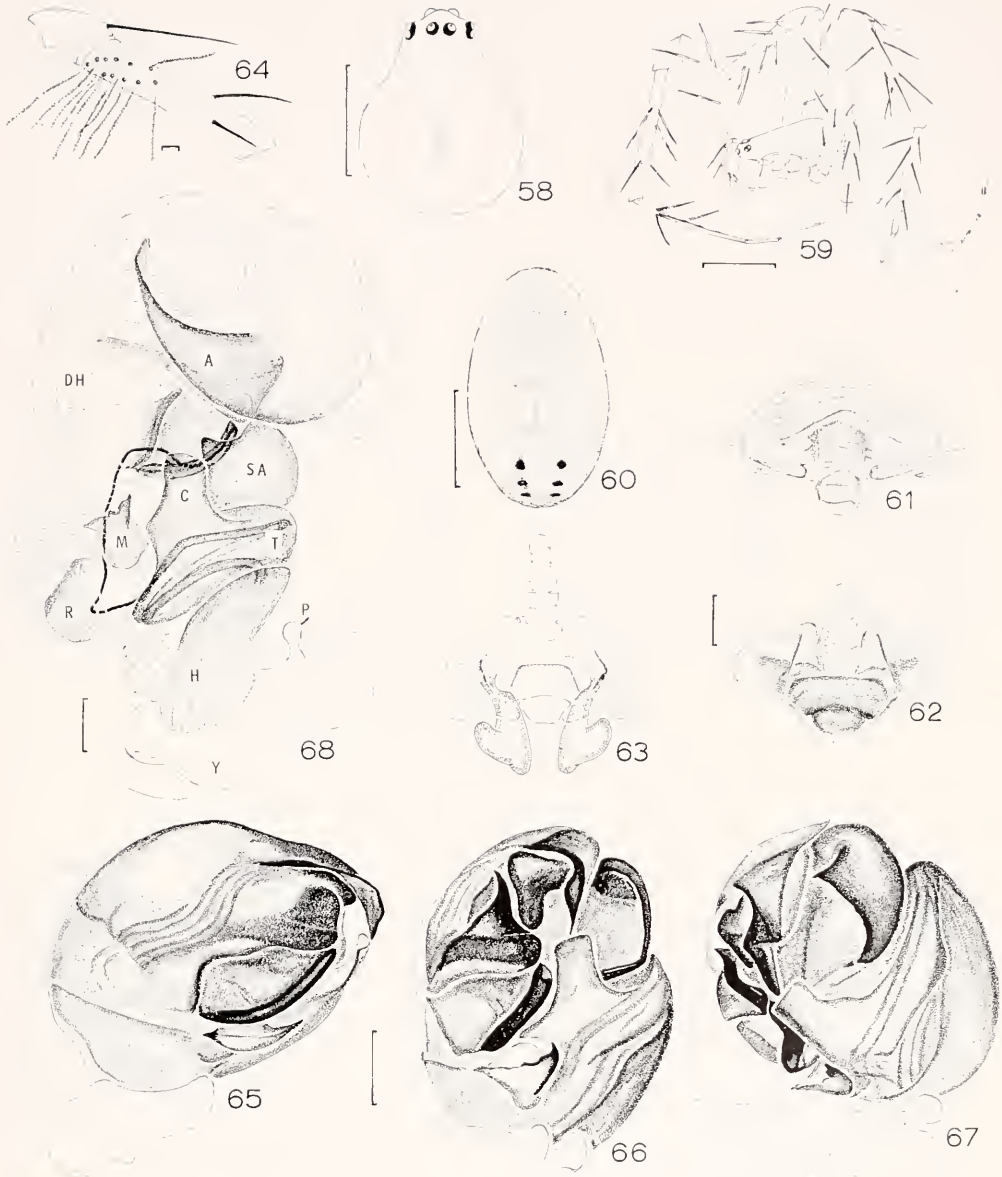
– No black longitudinal line on venters of first and second femora; abdomen marked with spots or patches. 3

2(1) Epigynum longer than wide in posterior view (Fig. 121); palpus with a long biforked embolus in mesal view (Figs. 125, 127); eastern United States ..... *gibberosa*

– Epigynum wider than long (Fig. 112); palpus not with biforked embolus, but two branches very short (Figs. 116, 117); southern Texas. ..... *fascialata*

3(1) Posterior median eyes larger than anterior medians; epigynum without scape but with median depression (Figs. 131, 133); palpus with long filiform embolus and terminal apophysis projecting in direction opposite to that of base of embolus (Figs. 140–144); southern Texas to Guatemala. ..... *calcarifera*

– Posterior median eyes subequal or smaller than anterior medians; epigynum with scape (Figs. 61, 69, 90); embolus short, terminal apophysis not projecting opposite base of embolus. 4



Figures 58–68. *Mangora maculata* (Keyserling). 58–64. Female; 58. Carapace, 59. Lateral view, 60. Abdomen, dorsal. 61–63. Epigynum; 61. Ventral, 62. Posterior, 63. Posterior cleared. 64. Female left third patella and tibia, prolateral. 65–68. Left palpus; 65. Mesal, 66. Ventral, 67. Ventro-lateral. 68. Expanded.

Abbreviations. A, terminal apophysis; C, conductor; DH, distal hematodocha; E, embolus; H, basal hematodocha; M, median apophysis; P, paracymbium; R, radix; SA, subterminal apophysis; T, tegulum; Y, cymbium.

Size indicators: 0.1 mm, except 58, 59, 60, 1.0 mm.

4(3) Spinnerets black, contrasting with light venter of abdomen; dorsum of abdomen with two inverted white comma-shaped marks (Figs. 75, 76); male terminal apophysis bent distally at tip (Fig. 79); epigynum as in Figs. 69–74; Arizona, New Mexico to Guatemala. ..... *passiva*

– Spinnerets not darker than venter of abdomen; dorsal abdominal marks otherwise; eastern United States and Canada. 5

5(4) Carapace without black median longitudinal line (Fig. 58); abdomen with three pairs of black spots posteriorly (Fig. 60); epigynum in posterior view with transverse sclerotized piece (Fig. 62); seminal receptacles not spherical (Fig. 63); palpus with terminal apophysis overhanging and almost touching conductor and embolus (Figs. 65–67). ..... *maculata*

– Carapace with median black longitudinal stripe (Fig. 96); abdomen marked with more anterior spots (Figs. 87, 95); epigynum and palpus otherwise. 6

6(5) Area between posterior abdominal spots black (Fig. 95); epigynum with a transverse sclerite on each side of scape (Fig. 90); median apophysis with only one spine (Figs. 100, 101); subterminal apophysis triangular with a thorn at base of conductor (Fig. 101); eastern U. S. ..... *placida*

– Area between posterior black abdominal spots gray (Fig. 87); epigynum with a longitudinal sclerite some distance from scape (Fig. 82); median apophysis with two spines (Figs. 88, 89); subterminal apophysis recessed between upper and lower lip (Fig. 89); Gulf States. ..... *spiculata*

Mangora maculata (Keyserling)
Figures 58–68; Map 4

Epeira maculata Keyserling, 1865, Verhandl. Zool. Bot. Ges. Wien, 15: 827, pl. 18, figs. 24–27, ♀, ♂. Female lectotypes here designated and one female paralectotype from Baltimore in the British Museum (Natural History). Six female and one male paralectotypes are *Metazygia incerta* (O. P.-Cambridge). Keyserling, 1893, Spinnen Amerikas, 4: 242, pl. 12, fig. 181, ♀, ♂.

Abbotia maculata, – McCook, 1893, American Spiders, 3: 241, pl. 20, figs. 9, 10, ♀, ♂.

Mangora maculata, – Comstock, 1912, Spider Book, p. 507. Comstock, 1940, Spider Book, rev. ed., p. 520. Roewer, 1942, Katalog der Araneae, 1: 775. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 239, fig. 757, ♀. Bonnet, 1955, Bibliographia Araneorum, 2: 2709. Grasshoff, 1971, Senckenbergiana Biol., 52: 295, fig. 48, ♂.

Mangora ornata, – Chamberlin and Ivie, 1944, Bull. Univ. Utah, Biol. Ser. 8(5): 105, fig. 8.

Note. Theridion ornatum is an old name that Chamberlin and Ivie (1944) attempted to resurrect for this species of *Mangora*. *Theridion ornatum* Walckenaer cannot be applied to this species. It is also a junior homonym of *T. ornatum* Hahn and was replaced by Roewer (1942) with *T. ornatulum*. The Abbot drawing, Walckenaer's type of *T. ornatum*, has a different abdominal pattern.

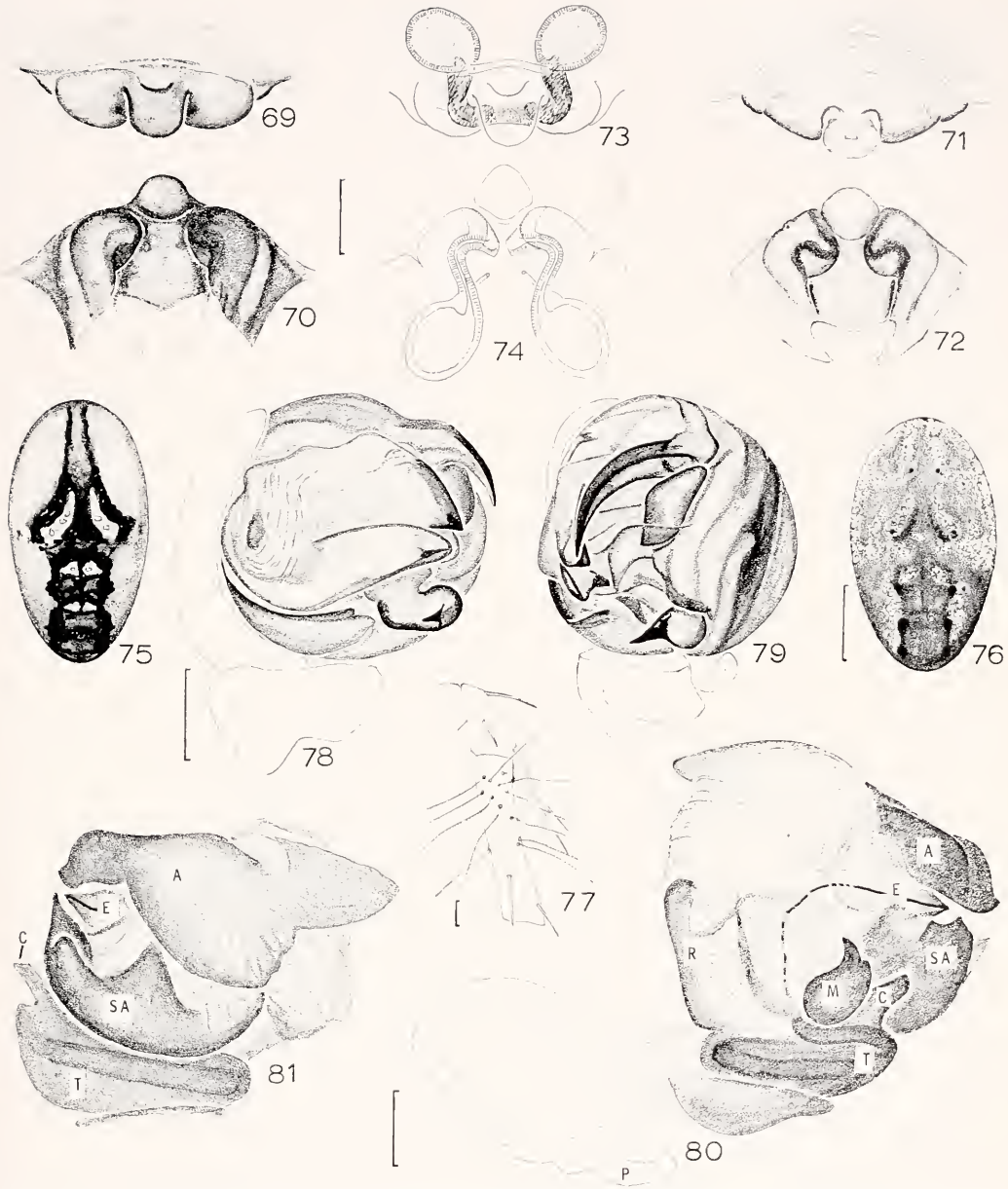
In collections many specimens are erroneously labeled *M. gibberosa*.

Description. Female from New Jersey: carapace, sternum, legs yellow-white. Dorsum and sides of abdomen with many white spots. There are three pairs of black patches posteriorly on the dorsum of the abdomen (Fig. 60). The venter has fewer white spots than the dorsum. The lateral eyes are 0.7 diameter of the medians, which are subequal in size. The anterior median eyes are one diameter apart, 1.5 from laterals. The posterior median eyes are slightly less than their diameter apart, 1.5 diameters from laterals. Total length 3.6 mm. Carapace 1.8 mm long, 1.4 mm wide. First femur, 2.3 mm; patella and tibia, 2.7 mm; metatarsus, 2.1 mm; tarsus, 1.0 mm. Second patella and tibia, 2.0 mm; third, 1.4 mm; fourth, 2.1 mm.

Male from New Jersey: coloration and eyes as in female. Total length 3.0 mm. Carapace 1.7 mm long, 1.3 mm wide. First femur, 2.1 mm; patella and tibia, 2.4 mm; metatarsus, 2.1 mm; tarsus, 1.0 mm. Second patella and tibia, 2.0 mm; third, 1.2 mm; fourth, 2.0 mm.

Variation. Females varied in total length from 3.6 to 5.5 mm; carapace 1.6 to 2.2 mm long, 1.3 to 1.7 mm wide. Males varied in total length from 2.7 to 4.0 mm; carapace 1.4 to 2.0 mm long, 1.2 to 1.6 mm wide.

Diagnosis. This common species lacks a median black line on the carapace (Fig.



Figures 69–79. *Mangora passiva* (O.P.-Cambridge). 69–74. Epigynum; 69, 71, 73. Ventral, 70, 72, 74. Posterior, 73, 74. Cleared. 69, 70, 73: (Syntype from Guatemala). 71, 72, 74: (Arizona). 75, 76. Female abdomen, dorsal; 75: (Guatemala). 76: (Arizona). 77: Female left third patella and tibia, prolateral. 78, 79. Left male palpus; 78. Mesal, 79. Ventral.

Figures 80–81. *Mangora placida* (Hentz), Left male palpus expanded; 80. Bulb, submesal view, 81. Bulb, lateral view.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; M, median apophysis; P, paracymbium; R, radix; SA, subterminal apophysis; T, tegulum.

Size indicators: 0.1 mm, except 75, 76, 1.0 mm.

58) and there are three pairs of black spots on the posterior part of the abdomen (Fig. 60). The epigynum in posterior view has a transverse sclerite (Fig. 62), the terminal apophysis of the palpus overhangs and almost touches embolus and conductor (Fig. 65).

Natural History. *Mangora maculata* has been collected in: a bog in Ontario, deciduous forest in Kansas, woods and shrubs and beech-maple dunes in Illinois, xero-mesic woods and edge of woods around fern-sedge-sumac swamp in Michigan, mesic woods in Virginia, flood plain forest in Tennessee, pine-hardwood bottom land in North Carolina, a ravine of a river in Georgia, flood plain hardwood forest in Louisiana. In Florida it has been found in tall grass and low brush, in dense woods, and in cypress on shore. Berry (1971, Amer. Midl. Natur. 85: 528) reports that immatures can be found most abundantly in June and July, adults from June and July until October in North Carolina.

Distribution. Eastern North America from Massachusetts, southern Ontario, northern Michigan to eastern Kansas, eastern Texas and northern Florida (Map 4).

Mangora passiva (O.P.-Cambridge)
Figures 69–79; Map 4

Epeira passiva O. P.-Cambridge, 1889. Biologia Centrali-Americana, Araneidea, 1: 20, pl. 5, fig. 4, ♀. Female syntypes from Cahabón [Alto Verapaz], San Juan [? Alto Verapaz], Chamelco [?], Tactic [Alto Verapaz], Chichochoc [?], Laguna de los Coheteros [?], Cobán [Alto Verapaz], all Guatemala in the British Museum (Natural History), examined.

Mangora passiva, – F. P.-Cambridge, 1904. Biologia Centrali-Americana, Araneidea, 2: 480, pl. 45, fig. 19, ♀. Roewer, 1942, Katalog der Araneae, 1: 774. Bonnet, 1955, Bibliographia Araneorum, 2: 2710.

Description. Female from Arizona: carapace with median longitudinal black line, eyes on black spot. Legs yellow, not banded, but with some dark spots at ends of articles. Dorsum of abdomen with a distinct pattern of upside-down comma-shaped marks (Figs. 75, 76). Sides below white band lacking pigment; a white pigment band on each side below pigmentless area. Venter with median longitudinal white spot and two pairs of white spots on each side of spinnerets. Spinnerets black. Posterior median eyes subequal to anterior medians, laterals about 0.9 diameter of anterior median eyes. Anterior median eyes their diameter apart, 1.4 diameters from laterals; posterior medians their diameter apart, slightly less than two from laterals. Total length 4.1 mm. Carapace 1.7 mm long, 1.5 mm wide. First femur, 2.0 mm; patella and tibia, 2.0 mm; metatarsus, 1.8 mm; tarsus, 0.7 mm. Second patella and tibia, 2.0 mm; third, 1.3 mm; fourth, 2.0 mm.

Male from Arizona: coloration of carapace as in female. Posterior half of dorsum of abdomen with three pairs of black spots, second and third pairs fused into longitudinal lines. There is a band of dorsal white pigment spots on each side. Venter without pigment, but spinnerets black. Secondary eyes 0.8 diameter of anterior medians. Anterior median eyes slightly less than one diameter apart, the same distance from laterals. Posterior median eyes their diameter apart, 1.5 diameters from laterals. Total length 2.3 mm. Carapace 1.3 mm long, 1.1 mm wide. First femur, 1.7 mm; patella and tibia, 1.7 mm; metatarsus, 1.6 mm; tarsus, 0.6 mm. Second patella and tibia, 1.5 mm; third, 1.0 mm; fourth, 1.4 mm.

Variation. Females vary in total length from 3.6 to 5.5 mm, carapace 1.7 to 2.0 mm long, 1.3 to 1.7 mm wide; males, total length 2.2 to 2.7 mm, carapace 1.3 to 1.5 mm long, 1.1 to 1.6 mm wide. Northern specimens are much lighter in color with only little black pigment (Fig. 76); specimens from central Mexico to Guatemala have a lot of black pigment on the dorsum of the abdomen, and the venter may have a median longitudinal white spot. There are also differences in the epigynum; it is less sclerotized in northern specimens with some wrinkles on the surface (Fig. 71),

smoother and more sclerotized in southern specimens (Fig. 69). Southern specimens appear to have the connecting ducts (Fig. 74) shorter and less looped than northern specimens. The measurements of a syntype from Cahabón are almost the same as those of the Arizona specimen.

Diagnosis. *Mangora passiva* can be separated from related species by the two inverted comma-shaped white marks on the dorsum of the abdomen (Figs. 75, 76). In the southwestern United States they can readily be separated by the light venter with contrasting black spinnerets. The epigynum in posterior view has diagnostic semicircular lips (Figs. 70, 72), and has large pear-shaped seminal receptacles (Fig. 74). The sickle-shaped terminal apophysis of the palpus (Figs. 78, 79) separates males of *M. passiva* from those of other species in the northern part of the range; the large subterminal apophysis (Fig. 79) separates *M. passiva* from the similar *Mangora bimaculata* (O. P.-Cambridge), in which this sclerite is very small.

Natural History. *Mangora passiva* has been collected by sweeping shrubs in oak-yellow pine woods, and from web in *Cornus* sp. near stream of the Santa Catalina Mts., Arizona, 1500–2300 m elevation.

Distribution. Arizona and New Mexico to Guatemala (Map 4).

Mangora spiculata (Hentz)
Figures 82–89; Map 4

Epeira spiculata Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 475, pl. 31, fig. 13, ♀. Female type from woods, Alabama, destroyed. Female neotype here designated from hammock woods, Dixie Graves Parkway, Baldwin County, Alabama, 10 March 1949 (A. F. Archer) in the American Museum of Natural History.

Mangora floridana Archer, 1951, Amer. Mus. Novitates, 1487: 14, figs. 31, 56, 60, ♀, ♂. Three male, one female syntypes from Peace River, west of Arcadia, Florida in the American Museum of Natural History, examined. NEW SYNONYMY.

Mangora spiculata, – Archer, 1951, Amer. Mus. Novitates, 1487: 46, fig. 27, ♀.

Mangora placida, – Archer, 1951, Amer. Mus. Novitates, 1487: 46, fig. 30, ♂.

Note. Ivie recognized this species as distinct and gave Archer his illustrations (Archer, 1951, figs. 56, 60), which Archer used, though he failed to recognize the diagnostic features of the species. Specimens determined by Archer as *floridana* are almost all *M. placida* (Hentz). Archer correctly determined specimens of this species *spiculata*, but wrote (1951) that the median apophysis has a single apical spur (a character of *M. placida*). I will follow Archer's determinations for the sake of stability of names, and have used as neotype of *Epeira spiculata* Hentz a specimen determined by Archer as *M. spiculata*. The name *Mangora placida* has been used continuously since the 1880's for a different, more common species having a wider range.

In various collections, most specimens of this species had been misidentified as *M. placida*.

Description. Female paratype of *M. floridana*: carapace yellowish; posterior median eyes with black eye rings and a median longitudinal dusky line, which is wider anteriorly. Thoracic area with a dusky margin on each side. Sternum yellowish with grayish on each side. Legs yellowish. Dorsum of abdomen with white pigment and posteriorly four pairs of round black spots; area between spots gray. Anteriorly there is a longitudinal line crossed by a transverse line without pigment (Fig. 87). Venter with a pair of longitudinal lines of white spots. Posterior median eyes 0.9 diameter of anterior medians. Anterior laterals 0.7, posterior laterals 0.8 diameter of anterior median eyes. Anterior median eyes their diameter apart, slightly less than one diameter from laterals. Posterior median eyes are one diameter apart, slightly more than one from laterals. Total length 2.4 mm. Carapace 1.13 mm long, 1.03 mm wide, 0.41 mm high. First femur, 1.41 mm; patella and tibia, 1.60 mm; metatarsus, 1.30 mm; tarsus, 0.59 mm. Second patella and tibia, 1.43 mm; third, 0.82 mm; fourth, 1.33 mm.

Male syntype of *M. floridana*: coloration

and structure as in female. Total length 1.9 mm. Carapace 1.13 mm long, 0.93 mm wide. First femur, 1.22 mm; patella and tibia, 1.38 mm; metatarsus, 1.08 mm; tarsus, 0.60 mm. Second patella and tibia, 1.18 mm; third, 0.67 mm; fourth, 0.96 mm.

Variation. Females varied in total length from 2.4 to 4.3 mm, carapace 1.1 to 1.7 mm long, 0.9 to 1.3 mm wide. Males varied in total length from 1.9 to 2.2 mm, carapace 1.1 to 1.2 mm long.

Diagnosis. The epigynum of *M. spiculata* differs from that of *M. passiva* in having a sclerotized piece on each side of the base in longitudinal direction (Figs. 82, 84), and the epigynum differs in posterior view in having the median soft area relatively larger (Fig. 83) than in *M. passiva.* The palpus of *M. spiculata* has a median apophysis with two points (Figs. 88, 89) and the subtegular apophysis lateral to the conductor has a recessed area (Fig. 89), while *M. placida* has only one point on the median apophysis and sclerotized piece lateral of the conductor is triangular with a thorn directed toward the base of the conductor.

Natural History. Mangora spiculata has been found in oak, pine hammock woods, in Alabama, low weeds and grass in Mississippi and tall grass, low brush and in dense undergrowth of wire grass in high pine-turkey oak woods in northern Florida. Males are mature in May in New Jersey, in June in Texas and North Carolina, January to July in Florida.

Distribution. Southeastern United States from New Jersey, Pennsylvania, southern Missouri to southern Texas; most common in northern Florida (Map 4); the northernmost record is from seven miles northwest of Gretna, Bass River State Forest, New Jersey; males and females, May, 1949.

Mangora placida (Hentz)
Figures 80, 81, 90–101; Map 4

Epeira placida Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 475, pl. 31, fig. 12, ♀. Female type from Alabama, destroyed. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 316, pl. 34, fig. 2, pl. 36, figs. 10, 13, ♀, ♂. McCook, 1893, Amer. Spiders, 3: 153, pl. 4, figs. 4, 5, ♀, ♂. Emerton, 1902. Common Spiders, 176, fig. 414.

Epeira praetrepida Keyserling, 1880, Verhandl. Zool. Bot. Ges. Wien, 30: 549, pl. 16, fig. 2, ♀. Female holotype from Georgia, in the Muséum National d'Histoire Naturelle, Paris, examined. Keyserling, 1893, Spinnen Amerikas, 4: 232, pl. 11, fig. 173, ♀.

Mangora placida, – Comstock, 1912, Spider Book, p. 505, fig. 544, ♀. Comstock, 1940, Spider Book, rev. ed., p. 518, fig. 544, ♀. Roewer, 1942, Katalog der Araneae, 1: 775. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 238, figs. 753–754, ♀, ♂. Archer, 1951, Amer. Mus. Novitates, no. 1487: 46, fig. 29, ♀. Bonnet, 1955, Bibliographia Araneorum, 2: 2710.

Mangora spiculata, – Archer, 1951. Amer. Mus. Novitates, no. 1487: 46, fig. 28, ♂. Misidentified, not *M. spiculata* (Hentz).

Note. I am not sure that this is the species Hentz illustrated, but this species has been called *M. placida* since 1884. The name *Mangora placida* has also been applied to specimens of *M. spiculata* in collections.

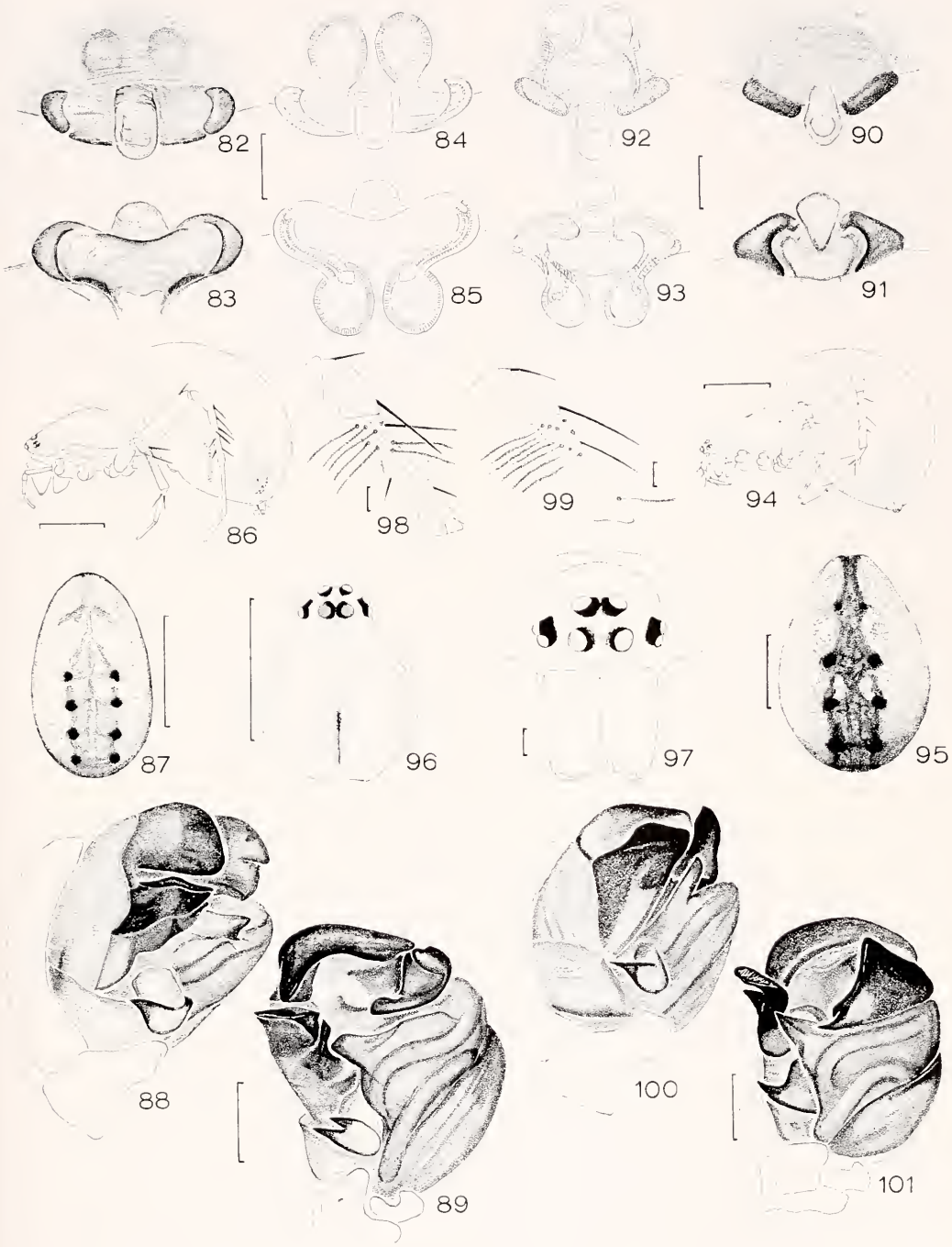
Description. Female from Michigan: carapace light brown, with a median dark line spreading out in eye area and becoming gray. Eyes ringed by black. Sternum light brown, dark around border. Legs light brown, with indications of bands and a light longitudinal gray line on venter. Dorsum of abdomen white with a median

→

Figures 82–89. *Mangora spiculata* (Hentz). 82–85. Epigynum; 82, 84. Ventral, 83, 85. Posterior, 84, 85. Cleared. 86. Female. 87. Female abdomen, dorsal. 88–89. Left male palpus; 88. Mesal, 89. Ventral.

Figures 90–101. *Mangora placida* (Hentz). 90–93. Epigynum; 90, 92. Ventral, 91, 93. Posterior, 92, 93. Cleared. 94. Female. 95. Female abdomen, dorsal. 96. Female carapace. 97. Eye area and chelicerae. 98, 99. Left third patella and tibia, prolateral; 98. Female, 99. Male. 100–101. Male palpus; 100. Mesal, 101. Ventral.

Size indicators: 0.1 mm, except 86, 87, 94, 95, 96, 0.1 mm.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dark line. The line is narrow in front, widest posteriorly, enclosing three pairs of black spots (Fig. 95). Sides white but black near spinnerets. Venter black in center with white on each side. The lateral eyes are slightly smaller than the medians. Anterior median eyes one diameter apart, one from laterals. Posterior median eyes slightly less than one diameter apart, one and one-quarter from laterals. Total length 3.6 mm. Carapace 1.4 mm long, 1.1 mm wide. First femur, 1.6 mm; patella and tibia, 1.6 mm; metatarsus, 1.2 mm; tarsus, 0.7 mm. Second patella and tibia, 1.5 mm; third, 0.9 mm; fourth, 1.4 mm.

Male: coloration like that of female except more contrasting and carapace darker. Eye arrangement like that of female. Total length 2.3 mm. Carapace 1.3 mm long, 1.0 mm wide. First femur, 1.3 mm; patella and tibia, 1.6 mm; metatarsus, 1.1 mm; tarsus, 0.7 mm. Second patella and tibia, 1.4 mm; third, 0.8 mm; fourth, 0.9 mm.

Variation. Females vary in total length from 2.3 to 4.5 mm, carapace 1.1 to 1.7 mm long, 0.9 to 1.3 wide. Males vary in total length from 2.0 to 2.8 mm, carapace 1.0 to 1.4 mm long, 0.8 to 1.1 mm wide.

Diagnosis. Unlike *M. spiculata,* the base of epigynum of *M. passiva* has two transverse, posterior sclerotized pieces (Fig. 90) and in posterior view the median soft area is smaller (Fig. 91) than that of *M. spiculata.* The palpus differs from that of *M. spiculata* in having a median apophysis with one point (Figs. 100–101) and a triangular sclerotized piece lateral to the conductor. The triangular piece has a thorn at the base pointing toward the conductor (Fig. 101). In *M. spiculata* this sclerite has a notch.

Natural History. Mangora placida has been collected from tree plantings in a sand dune area of North Dakota; from herb layer of deciduous forest in northern Wisconsin, New England, Virginia, and Texas; xero-mesic woods and woods around swamp in Michigan; mesic hammock, mixed forest to very dry woods in Florida. Males are mature from May to June in New England, May in New Jersey, November to February in Florida. Adult females can be found from May through the summer in northern states, in all seasons in Florida. Berry (1971, Amer. Midland Natur. 85: 528) reports that the species matures from March to May in North Carolina, earlier than *M. gibberosa* and *M. maculata,* but he probably confused two species under the name.

Distribution. Eastern United States, Maine and Ontario to North Dakota, southern Florida, southern Texas, northeastern Mexico. The southernmost locality is Linares, Nuevo Léon.

Mangora fascialata Franganillo
Figures 110–117

Mangora fascialata Franganillo, 1936, Los Aracnidos de Cuba, p. 83. Franganillo specimens from Cuba in Cuban Academy of Science, Havana, lack labels. Bonnet, 1956, Bibliographia Araneorum, 2: 2708.

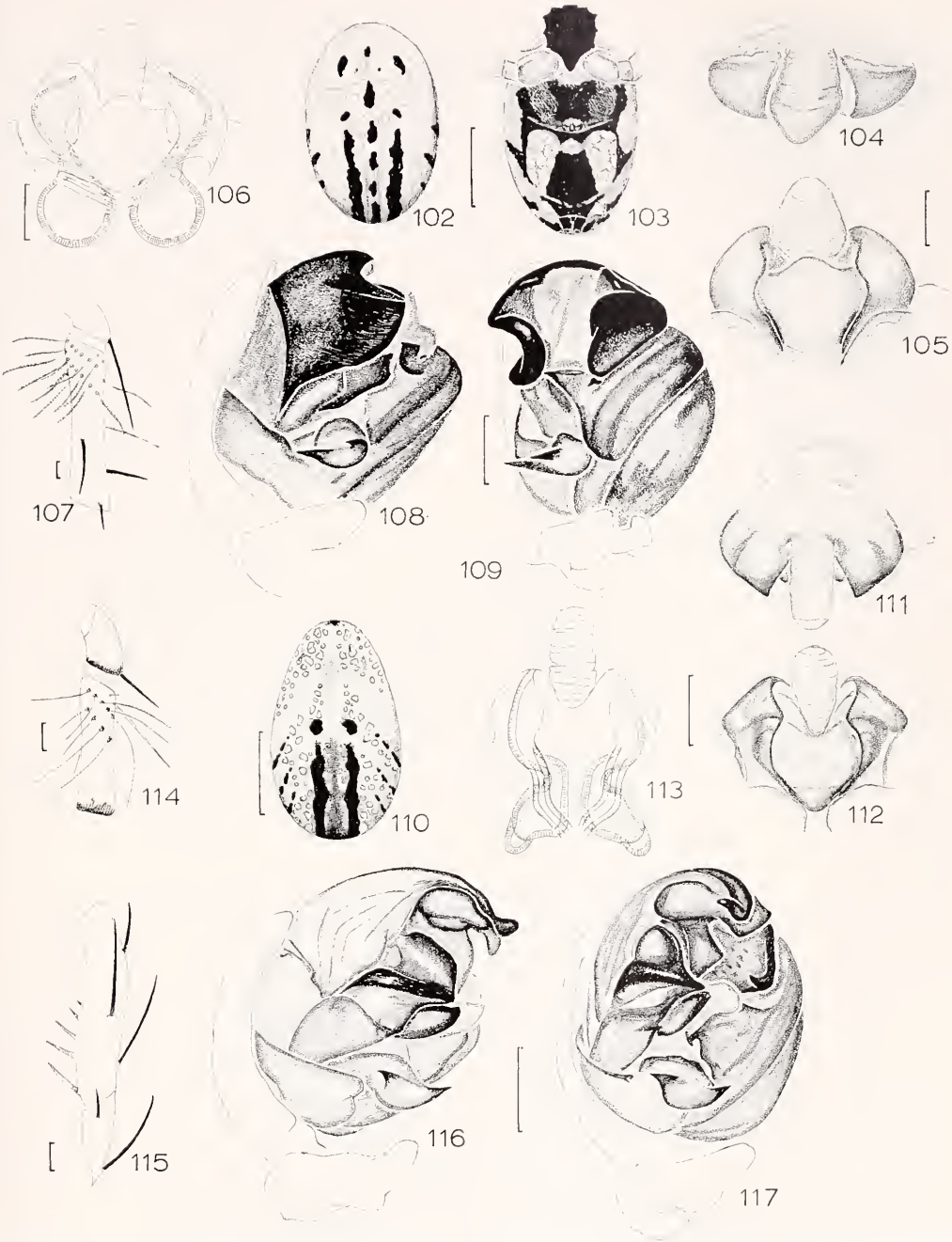
Mangora striatipes Bryant, 1945, Bull. Mus. Comp. Zool., 95: 375, figs. 17, 18, ♀, ♂. Male holotype from Puerto Plata, Dominican Republic, in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Mangora gibberosa, – Kraus, 1955, Abhandl. Senckenberg, Naturf. Gesell. 493: 22, figs. 57, 58, ♀. Not *M. gibberosa* (Hentz).

Mangora conspicua Chickering, 1963, Breviora, Mus. Comp. Zool., 191: 2, figs. 1–7, ♀, ♂. Female holotype from El Potosí, Cerro Potosí, Nuevo Léon, Mexico in the Museum of Comparative Zoology, examined. NEW SYNONYMY.

Note. Franganillo lists three species of *Mangora* for Cuba; but only one species is in North American collections; there is no evidence that either *M. placida* or *M. picta* occurs on the island. Even if they do, *M. fascialata* is the most common species. Franganillo compares *M. fascialata* with *M. acalypha,* further evidence that this species was the subject of his poor description, lacking both illustration and labeled type.

Description. Female from Edinburg, Texas: carapace yellow-white with a median longitudinal black line, a black line around margin of thorax on each side, eyes



Figures 102–109. *Mangora acalypha* (Walckenaer) of Europe. 102. Female abdomen, dorsal. 103. Female abdomen and sternum, ventral. 104–106. Epigynum; 104. Ventral, 105, 106. Posterior, 106. Cleared. 107. Female left third tibia, prolateral. 108, 109. Left male palpus; 108. Mesal, 109. Ventral.

Figures 110–117. *Mangora fascialata* Franganillo. 110. Female abdomen, dorsal. 111–113. Epigynum; 111. Ventral, 112, 113. Posterior, 113. Cleared. 114. Female left third patella and tibia, prolateral. 115. Male left second tibia, prolateral. 116, 117. Male palpus; 116. Mesal, 117. Ventral.

Size indicators: 0.1 mm, except 102, 103, 110, 1.0 mm.

ringed by black. Sternum black, yellow in middle. Legs with black longitudinal ventral line on first and second femurs, and black spots and narrow rings on other articles. Posteriorly, dorsum of abdomen has a pair of longitudinal black lines (Fig. 110), with dark between lines; anteriorly there is a small median black spot. Dark areas are surrounded by white pigment spots. Sides have anterior black patches, and posterior dorsal lines go toward sides anteriorly. Venter black between epigynum and spinnerets, with a longitudinal white pigment line on each side. There is a transverse black line in front of spinnerets. The posterior spinnerets are black on the sides and the anal tubercle is black posteriorly. Diameter of posterior median eyes 1.1 diameters of anterior medians, laterals about 0.9 diameter of anterior medians. Anterior median eyes slightly more than their diameter apart, the same distance from laterals. Posterior median eyes their diameter apart, 1.7 diameters from laterals. Total length 3.6 mm. Carapace 1.4 mm long, 1.0 mm wide, 0.5 mm high. First femur, 1.5 mm; patella and tibia, 1.6 mm; metatarsus, 1.4 mm; tarsus, 0.7 mm. Second patella and tibia, 1.4 mm; third, 0.8 mm; fourth, 1.4 mm.

Male from Texas: coloration as in female, but venter of abdomen without black or white pigment. Diameter of posterior median eyes 0.8 diameter of anterior medians, anterior laterals 0.6, posterior laterals 0.5 diameter of anterior median eyes. Anterior median eyes 0.6 diameter apart, 0.6 diameter from laterals. Posterior median eyes 0.7 diameter apart, 1.5 diameters from laterals. The second tibia is slightly curved and has a row of five macrosetae, proximally toward the inside (Fig. 115). Total length 2.0 mm. Carapace 1.2 mm long, 0.9 mm wide, 0.5 mm high. First femur, 1.4 mm; patella and tibia, 1.4 mm; metatarsus, 1.1 mm; tarsus, 0.6 mm. Second patella and tibia, 1.1 mm; third, 0.7 mm; fourth, 1.1 mm.

Variation. Females varied in total length from 3.2 to 3.6 mm. Carapace 1.3 to 1.6 mm long, 1.0 to 1.2 mm wide.

Diagnosis. As in *M. gibberosa*, but unlike other species, there are lines on the venter of the first two pairs of femora. *Mangora fascialata* differs from *M. gibberosa* by not having the long biforked embolus in the male palpus (Figs. 116–117), and by having the epigynum in posterior view about square (Fig. 112). The seminal receptacles have a lobe (Fig. 113). Those of *M. gibberosa* are oval. The diagnostic features are the median area of the epigynum whose outline is bottle-shaped in posterior view (Fig. 112), and the distal curl of the terminal apophysis of the palpus (Figs. 116, 117).

Natural History. The species has been collected from herbs and shrubs of live oak thicket, in cane and mesquite along river in southern Texas, by sweeping from weeds and acacia near road in Nuevo Léon. Females have been collected from April to December, males in June, July and November.

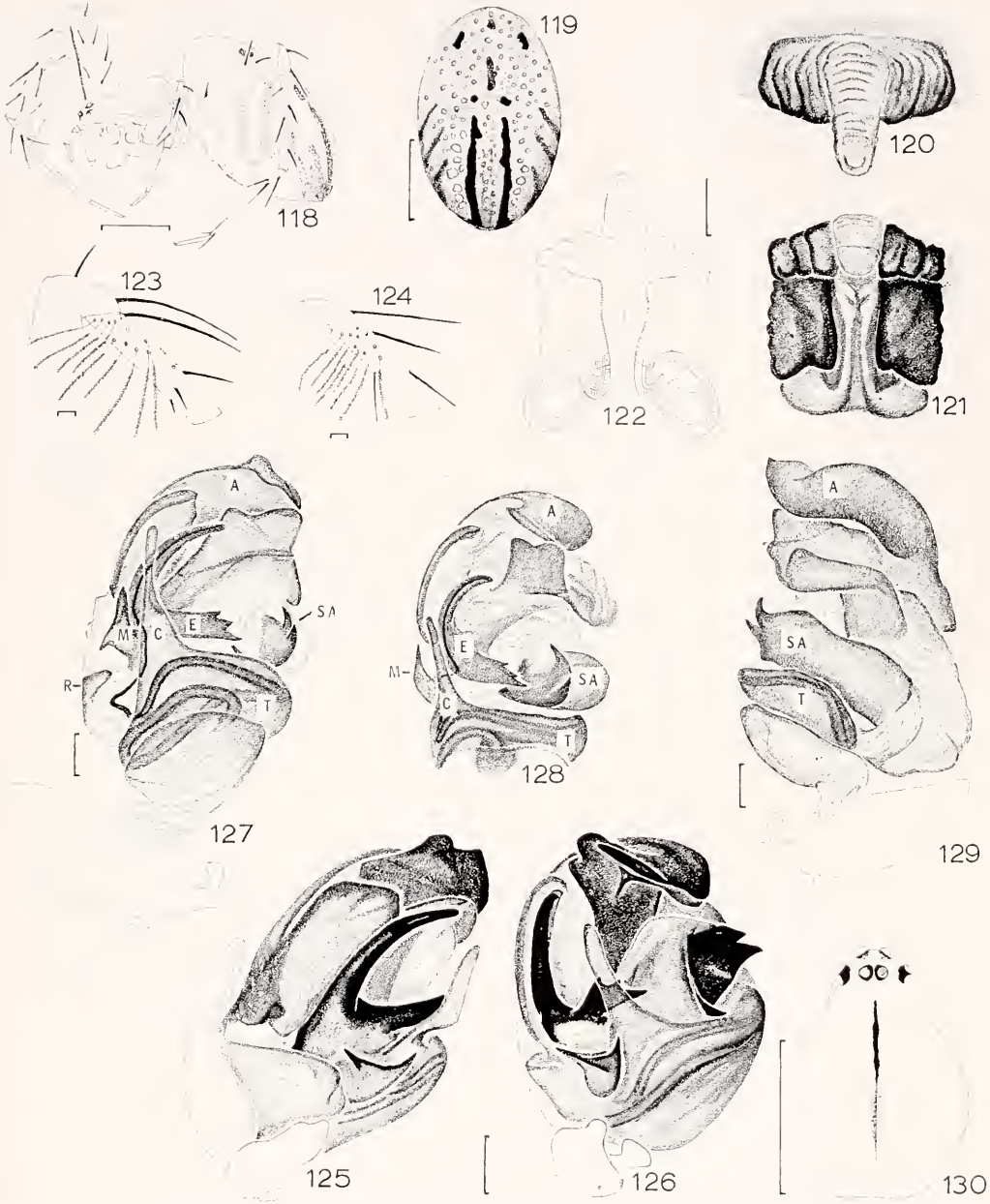
Distribution. Southern Texas, Baja California to El Salvador and Honduras, Hispaniola and Cuba. It has not been found in southern Florida although it may occur there (Map 4).

Mangora gibberosa (Hentz)
Plate 2; Figures 118–130; Map 4

Epeira gibberosa Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 477, pl. 31, fig. 20, ♀. Types from Alabama in Boston Society of Natural History, destroyed. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 317, pl. 34, fig. 1, pl. 36, fig. 17, ♀, ♂. Keyserling, 1893, Spinnen Amerikas, 4: 241, pl. 12, fig. 180, ♀, ♂. Emerton, 1902, Common Spiders, p. 175, figs. 411–413, ♀.

Abbotia gibberosa, – McCook, 1893, American Spiders, 3: 240, pl. 20, figs. 7, 8, pl. 24, fig. 4, ♀, ♂.

Mangora gibberosa, – Comstock, 1912, Spider Book, p. 505, figs. 541–543, ♀, web. Comstock, 1940, Spider Book, rev. ed., p. 518, figs. 541–543, ♀, web. Roewer, 1942, Katalog der Araneae, 1: 775. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 239, figs. 743–744, 755–756, 2042, ♀, ♂, web. Bonnet, 1955, Bibliographia Araneorum, 2: 2708.



Figures 118–130. *Mangora gibberosa* (Hentz). 118. Female. 119. Female abdomen, dorsal. 120–122. Epigynum; 120. Ventral, 121, 122. Posterior, 122. Cleared. 123. Female, left third patella and tibia, prolateral. 124. Male, left third patella and tibia, prolateral. 125–129. Left male palpus; 125. Mesal, 126. Ventral, 127–129. Expanded, 127. Ventral, 128. Ventro-lateral, 129. Lateral. 130. Carapace of female.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; M, median apophysis; R, radix; SA, subtegular apophysis; T, tegulum.

Size indicators: 0.1 mm, except Figures 119, 130, 1.0 mm.

Mangora ornata, – Archer, 1951, Amer. Mus. Novitates, 1487: 15, fig. 26, ♂. Erroneous determination, not *Theridion ornatum* Walckenaer. The latter name also is a junior homonym and was replaced by Roewer (1942) with *T. ornatulum*.

Description. Female from Wisconsin: Carapace, sternum, legs yellow-white, carapace with black median thoracic line, black rings around eyes. A longitudinal, ventral black line on the first and second femora (Fig. 118). Dorsum of abdomen with three longitudinal lines as shown in Figure 119. Sides with about four diagonal dark marks going from anterodorsal to posteroventral. Venter gray in center. Lateral eyes very slightly smaller than medians. Anterior median eyes less than one diameter apart, slightly more than one from laterals. Posterior median eyes about their radius apart, two diameters from laterals. Total length 4.0 mm. Carapace 1.8 mm long, 1.4 mm wide. First femur, 2.1 mm; patella and tibia, 2.3 mm; metatarsus, 1.8 mm; tarsus, 0.6 mm. Second patella and tibia, 2.0 mm; third, 1.2 mm; fourth, 2.0 mm.

Male: Coloration as in female. Carapace narrower in front than in female. Eye sizes similar to those of female. Anterior median eyes one diameter apart, slightly more than one from laterals. Posterior median eyes slightly less than one diameter apart, 1.5 diameters from laterals. Total length 2.6 mm. Carapace 1.5 mm long, 1.2 mm wide. First femur, 1.9 mm; patella and tibia, 2.0 mm; metatarsus, 1.7 mm; tarsus, 0.8 mm. Second patella and tibia, 1.7 mm; third, 1.1 mm; fourth, 1.7 mm.

Variation. Females vary in total length from 3.4 to 4.8 mm, carapace 1.4 to 1.9 mm long, 1.2 to 1.5 mm wide. Males vary in total length from 2.6 to 3.2 mm, carapace 1.5 to 1.7 mm long, 1.2 to 1.4 mm wide.

Diagnosis. The black lines on the venter of the first and second femora (Fig. 118) distinguish *M. gibberosa* from all other North American species except *M. fascialata*. In posterior view the epigynum of *M. gibberosa* is longer than wide with the borders of the median soft area parallel (Figs. 121, 122), that of *M. fascialata* is square with the outline of the median soft area bottle-shaped. The seminal receptacles of *M. gibberosa* are oval (Fig. 122), those of *M. fascialata* have a lobe. The palpus of *M. gibberosa* has a unique two-pronged sclerotized embolus on the mesal side (Figs. 125–127).

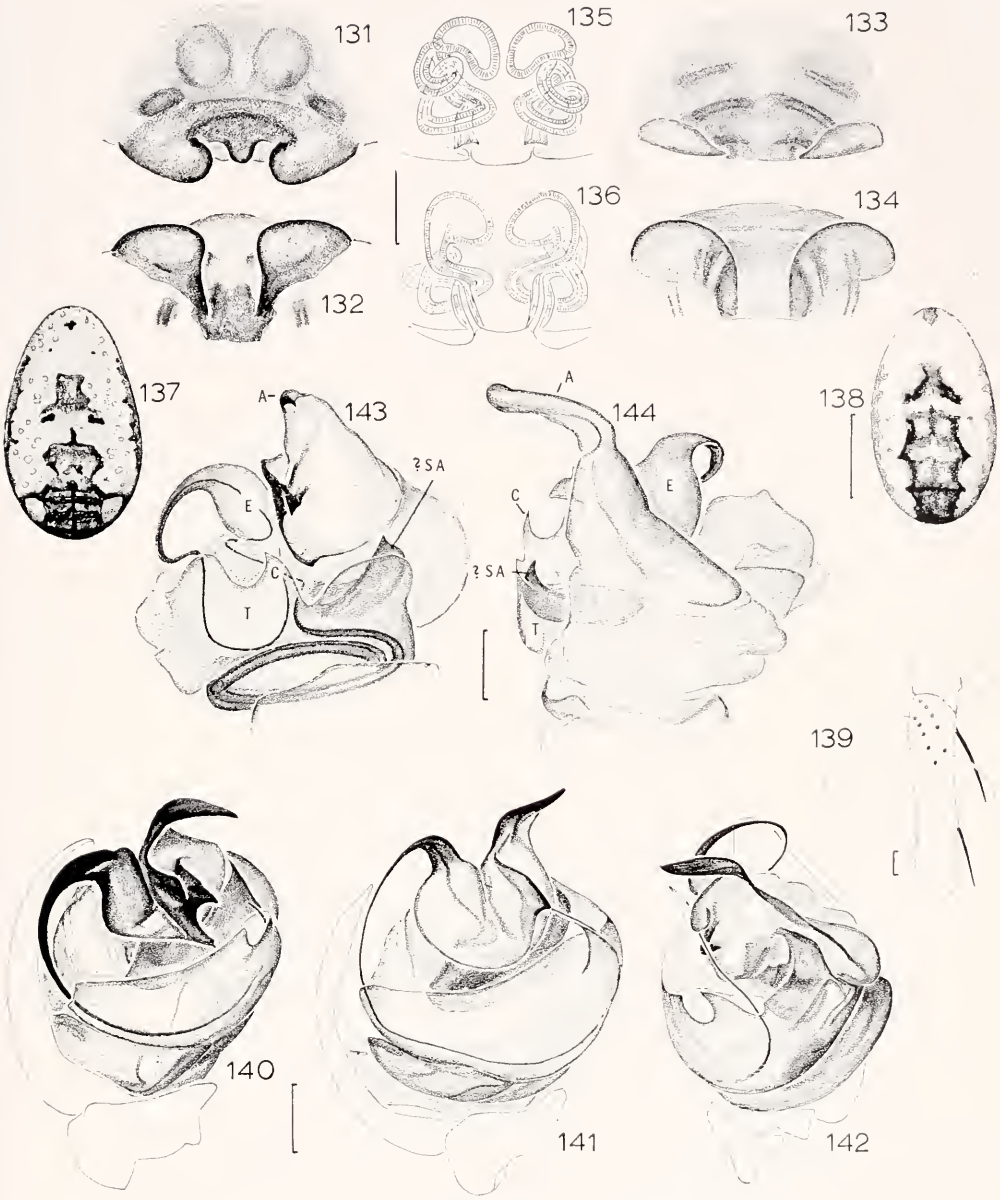
Natural History. Mangora gibberosa, unlike the three other common species in the eastern states, is more common in fields than in woods. It has been collected in herbs of deciduous forest in Kansas; in tall grass, deciduous woods and herbs in an orchard in Ontario; in upland forest in an old field, and along a road in Michigan; along a forest edge in New England; in a meadow in Georgia; in tall grass, in an old field, in low brush, and in dense undergrowth of high pine-turkey oak woods in Florida. Males are mature in July in northern Wisconsin, July and August in New England, June to September in New Jersey, May to June in Texas, April in Florida. Berry (1971, Amer. Midland Natur. 85: 528) had mature specimens from May to November in North Carolina. Adult females are found from June to September in the northern states, and April to November in Florida.

Kaston (1948) pictured the web (fig. 2042) with 50 to 60 radii and as many viscid strands below the hub. The web is 30 to 40 cm in diameter (Plate 2). The eggs are placed in rolled-up leaves. According to Kaston (1948), the eggs hatch in fall and the spiderlings leave the cocoon in spring.

Distribution. Eastern North America (Map 4) from Maine, southern Ontario, North Dakota to southern Florida and southern Texas.

Mangora calcarifera F.O.P.-Cambridge
Figures 131–144; Map 4

Mangora calcarifera F. O. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 479, pl. 45, figs. 12, 13, ♀, ♂. Two female, two male syntypes from Petexbatún, Guatemala in



Figures 131–144. *Mangora calcarifera* F.O.P.-Cambridge. 131–136. Epigynum; 131, 133, 135. Ventral, 132, 134, 136. Posterior, 135, 136. Cleared. 137, 138. Female abdomen, dorsal. 139. Female left third patella and tibia, prolateral. 140–144. Left male palpus; 140, 141. Mesal, 142. Ventral. 140: (Texas). 141, 142: (Guatemala). 143, 144: Expanded.

Abbreviations. A, terminal apophysis; C, conductor; E, embolus; ?SA, ?subterminal apophysis; T, tegulum.

Size indicators: 0.1 mm, except Figures 137, 138, 1.0 mm.

the British Museum, Natural History, examined. Bonnet, 1955, Bibliographia Araneorum, 2: 2708.

Description. Female syntype: Carapace yellow with a median dorsal longitudinal line and a lateral longitudinal band on each side in thoracic region; black rings around posterior median eyes. Legs not banded. Dorsum of abdomen with black marks as illustrated (Figs. 137, 138), and lacking white pigment spots. Sides of abdomen with two dark patches, one posterior to the other. Venter with only a black mark anteriorly and around spinnerets. Diameter of posterior median eyes 1.2 diameters of anterior medians. Lateral eyes 0.9 diameter of anterior median eyes. Anterior median eyes slightly less than their diameter apart, 0.7 diameter from laterals. Posterior median eyes slightly less than their diameter apart, slightly less than one from laterals. Total length 3.7 mm. Carapace 1.4 mm long, 1.2 mm wide, 0.7 mm high. First femur, 1.6 mm; patella and tibia, 1.8 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm. Second patella and tibia, 1.5 mm; third, 1.0 mm; fourth, 1.6 mm.

Male: less distinctly colored than female. Eyes similar to those of female except laterals are relatively smaller than those of female. Anterior median eyes slightly less than their diameter apart, slightly less than their diameter from laterals. Posterior median eyes 1.2 diameters apart, slightly less than their diameter from laterals. Total length 2.4 mm. Carapace 1.3 mm long, 1.0 mm wide. First femur, 1.4 mm; patella and tibia, 1.6 mm; metatarsus, 1.3 mm; tarsus, 0.7 mm. Second patella and tibia, 1.4 mm; third, 0.9 mm; fourth, 1.4 mm.

Diagnosis. Mangora calcarifera is readily separated from other *Mangora* north of Mexico by the large posterior median eyes, by the lack of a scape in the epigynum (Figs. 131, 133), and by the long filiform embolus in the palpus (Figs. 140–143). *Mangora calcarifera* can easily be confused with *M. trilineata,* also common in Mexico, and also having large posterior median eyes. However, in *M. trilineata* O. P.-Cambridge, the relatively large seminal receptacles show through the surface of the epigynum and there are short connecting ducts, and the male has a shorter embolus.

Variation. Northern specimens have less pigment and are lighter than those from central Mexico and Central America. The palpi show differences which may be geographic.

Natural History. The species was collected in a palm grove in southern Texas and from a river floodplain in Tamaulipas. Mature males have been found in March and September in Texas, July in San Luis Potosí, and April in Honduras.

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The Prothorax of Coleoptera: (Except Bostrichiformia - Cucujiformia)

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THE PROTHORAX OF COLEOPTERA: (EXCEPT BOSTRICHIFORMIA-CUCUJIFORMIA)

T. F. HLAVAC[1]

ABSTRACT. Variation in prothoracic structure is documented for a portion of the Polyphaga and for the three other suborders of Coleoptera. The structural diversity detected through examination, and usually dissection, of over 350 genera is presented in 166 figures representing 121 genera.

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INTRODUCTION

The prothorax is the most variable element of the extremely diverse locomotory system of Coleoptera. Parallelism and convergence are dominant themes in prothorax evolution. For this reason, characters of high weight are not common. However, comparison of transformation series between higher taxa can yield improved hypotheses on both phyletic and biological diversification of the higher categories of beetles (Hlavac, in press). Such inferences need to be based on prior analysis of within-group variation. This type of basic data on comparative structure is presented below; the Cucujiformia are to be treated in a similar fashion.

An introduction to morphology and the major elements of variation of the coleopterous prothorax is given elsewhere (Hlavac, 1972).

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Throughout the course of this research, Professor F. M. Carpenter has provided inspiration and not a little wisdom.

MATERIALS AND METHODS

The number of forms dissected within a higher taxon depended roughly on a group's size and systematic complexity as well as on the amount of variation detected. Variation was estimated by routine dissection of common genera and in external examination of specimens from a nearly complete synoptic collection of beetle tribes.

Usually three dry, determined specimens per species were relaxed in hot water and removed from pins or points. The prothoraces of two examples were isolated while the whole relaxed third specimen was placed in alcohol along with the heads and remaining parts of the other two. Detached structures were treated in warm 10% potassium hydroxide for about five minutes and then flushed with a stream of water from a hypodermic syringe. If large amounts of solid muscle tissue remained, treatment continued until the tissue was soft enough to be flushed out. After the pericoxal membrane was ruptured and the coxa was moved laterally, one prothorax was sliced parasagittally with a razor blade leaving the sternal projection untouched. If the notopleural joint was membranous, the pleuron and coxa were then detached from the smaller section. The larger section was then examined in lateral view. If the internal boundaries of the endopleuron, sternal and notal rim-folds, as well as the enclosed portions of the coxa and trochantin, were not readily visible in very strong transmitted light, the section was bleached and cleared along with the unsectioned prothorax in hydrogen peroxide with a few drops of KOH. The detached pleuron and coxa were cleared separately, or if necessary, stained with Chlorazol Black.

The standard study series then consisted of: one whole relaxed specimen, one whole cleared prothorax, and one sectioned cleared prothorax with pleuron and coxa detached on one side. Routine outline drawings of lateral views were done using the sections and were checked with the non-KOH'd specimen to correct any distortion caused by processing.

Depending on size, dissected prothoraces as well as other parts were placed in glycerine and studied in plant-quarantine type watch glasses or in low-form Stender dishes. For detailed study and drawing, dissected parts were positioned in a layer of fine sand at the bottom of a glycerine-filled container.

Drawings were made with a grid mounted in the 12.5× eyepiece of a Leitz dissecting scope. The most informative single view of a beetle thorax is a lateral one parallel to the coxal long axis; figures of entire prothoraces included here are drawn in this position.

Suborder **ARCHOSTEMATA**

CUPEDIDAE

Figures 1–4, 141

Pleuron large, rigid; forms lateral wall of prothorax. Anterior pleural flange small, external, or enclosed, or absent with an internal fold. Trochantin motile, external.

Head prognathous, posterior aspect enclosed by prothorax. Cervical sclerites

absent. Sternal flange with paired internal regions, as in Adephaga.

Anterior pleural fold, including the flange, visible externally only in *Priacma* (Figs. 1, AFL), it is enclosed by the notum in *Prolixocupes* and *Cupes* (Fig. 2). In *Tetraphalerus* and *Omma* (Figs. 3, 4) the anterior pleural fold is reduced and internalized by a lobe on the sternal flange. The anterior configuration of *Tetraphalerus* and *Omma* is similar to that of the Adephaga (Hlavac, 1972, figs. 10–14).

The anterior rim-fold in the cupedines is divided into two regions by the origin of the cervical membrane, the anterior region is the pleural flange. In *Prolixocupes* and *Priacma* (Hlavac, 1972, figs. 2, 11–13) the pleural flange is long and slender, it rests on but is not attached to the sternum. In *Cupes*, however, the flange is short, squat and is attached to the sternum by an anterior extension of the pleurosternal joint.

Sternal attachment region of the ventral pleural rim-fold present only in the cupedines, where the joint is long, straight and tightly membranous, and is either horizontal or slightly inclined. In *Tetraphalerus* the very long, curved pleurosternal joint is solid anteriorly with a distinct suture but without rim-folds, while posteriorly it appears semimembranous with pleural and sternal folds. The sternum and pleuron of *Omma* are solidly fused together, no suture is present.

Pleurotrochantinal joint membranous, external in the cupedines but in the ommadines it is concealed by the broad ventral surface of the pleural fold which forms a small trochantinal cowling.

Below the endopleural invagination, which is the actual site of membranous notopleural attachment, a notal rim-fold surface overlaps, conceals and may articulate with a section of the pleuron as in Myxophaga. The band of enclosed pleuron is broadest in *Cupes*, less so in *Priacma* and quite narrow in ommadines, and is less heavily pigmented than surrounding external regions and lacks setae. Overlap continues behind the endopleuron, but consists here of the margins of posterior folds or flanges, and the enclosed pleuron is setose and has normal pigmentation. Boundary of overlap sometimes marked by a slight carina on the pleuron. Evans (1974) has incorrectly identified this carina as a "pleural ridge" that is an apophysis or invagination homologous to that found in other holometabolous orders, but absent in Coleoptera. Posterior flange extends behind coxa to overlap and interlock with the mesepisternum, flange largest in ommadines.

Endopleuron small, flat in cross section, does not come near the dorsal wall of the notum.

Trochantin triangular and external (cupedines) or quadrate and partially enclosed (ommadines). Sternotrochantinal joint loosely membranous. The trochantin is capable of mediolateral movement about the pleural attachment.

In the cupedines the sternal projection extends below and slightly behind the coxae, e.g., *Priacma*, while in the ommadines it is small and extends between the coxae.

Coxa squat, articular region very large (about .6 total length), only a small amount of which is enclosed by the pleuron (Fig. 14).

In the cupedines, the sternal projection extends below the coxal apex, the coxae are partially housed by the cryptosternum and by large cavities in the mesepisternum. The coxal rotation axis is parallel to the long axis; coxal motion is restricted to simple rotation. The coxal mechanism of *Omma* may be similar to that of the cupedines. In *Tetraphalerus* the coxal apex extends far below the very small projection and posteriorly the coxae are not enclosed by mesepisternal cavities. In addition, the sternellum bears a pair of large condyles just below the trochantinal apex that are inserted into cavities in the coxae. The rotation axis extends from the pleurocoxal to the sternocoxal articulation and is not parallel to the long axis. Since the coxal

apex is free and the rotation axis is not aligned with the long axis, the coxal apex moves anteroposteriorly as the coxa rotates.

There are two different types of propleuron-mesepisternal interlocking devices in the Cupedidae. In the cupedines, the posterior fold of the pleuron is expanded into a condyle above the coxal articulation that is placed into a cavity on the mesepisternum. In the ommadines, the cavity is on the pleuron and the condyle on the mesepisternum. The prosternal projection fits into a small (*Priacma*) or large (*Cupes*) fossa on the mesosternum. It is possible the notum may be motile around the pleuron, such movements could help clamp the prothorax onto the mesothorax.

The anterior configurations of *Cupes* and *Prolixocupes* on one hand and the ommadines on the other can be derived along two pathways from a *Priacma*-like configuration. Each pathway involves reduction and either enclosure or internalization of the anterior pleural fold. The similarity of the anterior configurations of Adephaga and the ommadines raises questions on the possible relationships between these groups or on the likelihood of parallel development.

The lack of a large sternal projection in the ommadines, especially *Tetraphalerus*, may not be primitive but may be part of a specialized mechanism to permit anteroposterior movement of the coxal apex. The trochantin of the ommadines is more enclosed by the pleuron and sternum and may be more motile than that of cupedines.

MICROMALTHIDAE
Figure 5

A uniquely simplified configuration, endopleuron absent, notum, pleuron, trochantin and sternum fused together without even the slightest vestige of sutures.

Head prognathous, completely enclosed posteriorly by the prothorax, cervical sclerites absent. Notum, pleuron, trochantin and sternum solidly fused together, sutures absent. Posterior flange expanded into a small condyle that articulates with the concave dorsal face of the coxa. Coxa rests against but does not articulate with the dorsally curved posterior rim of the prosternum. Posteriorly, the coxae are housed in large, divided, mesosternal cavities. A small projection on the coxa near the apex fits into a groove on the ventral rim of the mesosternal concavity to form a procoxa-mesosternal articulation. Sternellum small, vertical, quadrate.

Suborder **ADEPHAGA**
Figures 6–12, 142–143, 149–158

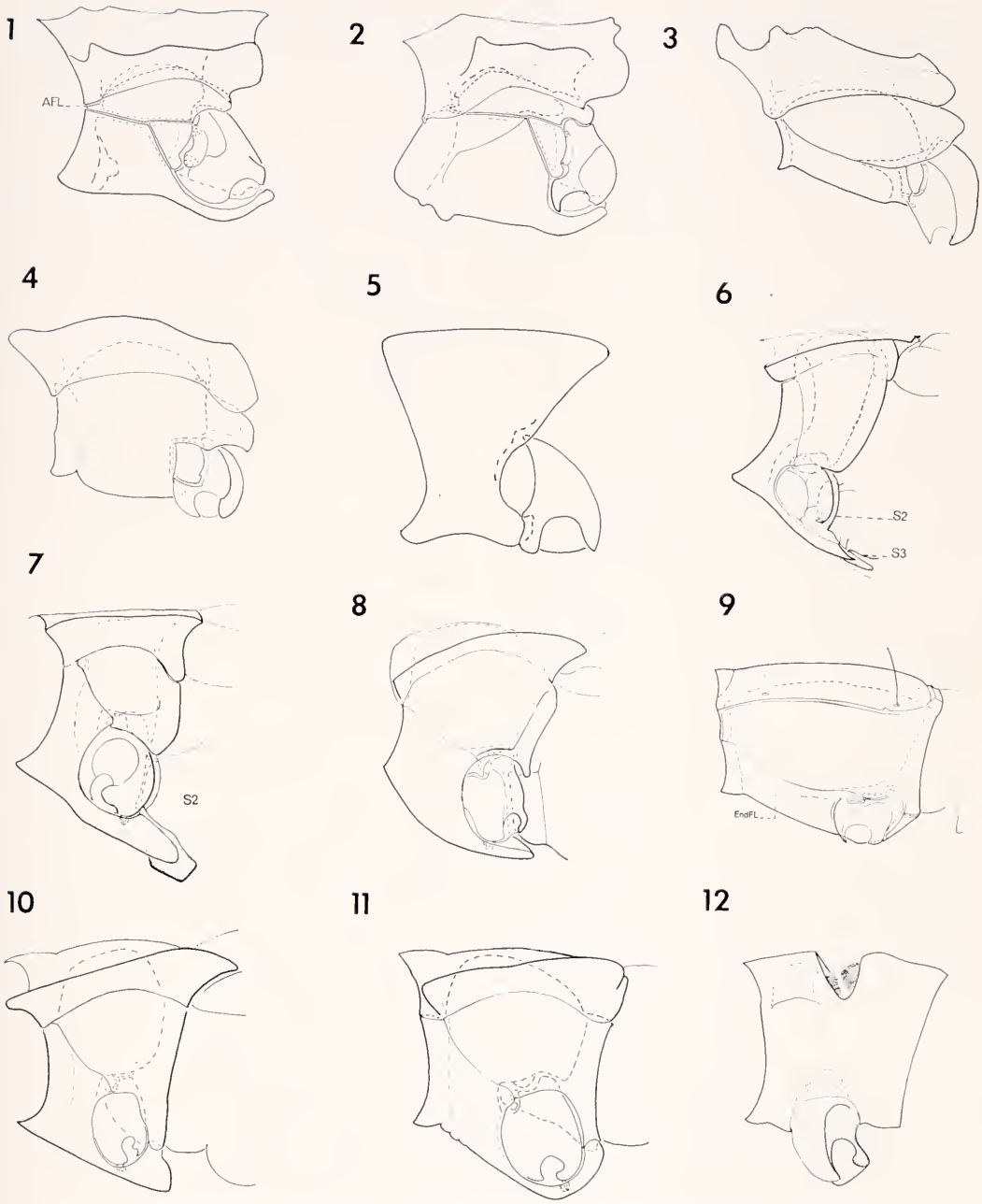
Pleuron a prominent part of body wall, rigid. Anterior pleural fold internal. Trochantin small, motile, enclosed.

Head usually prognathous and deeply

→

Abbreviations Used in Figures

AF, anterior fold, of pleuron.
AFL, anterior flange, of pleuron.
Artic, articular region of coxa.
CRN, crenulations.
CrS, cryptosternum.
Cw, cowling.
CxBr, post coxal bridge.
EndFL, endoflange.
EndPL, endopleuron.
ICxSP, intercoxal septum.
Invg, endopleural invagination.
LCnd, lateral condyle of notum.
MCnd, median condyle of notum.
NCnd, notal condyle, coxal articular.
NCw, notal cowling.
NPj, notal projection.
PL, pleuron.
PLCnd, pleural condyle, coxal articular.
PLPj, pleural projection.
PL-RFM, pleural rim-fold margin.
Pr, proprioreceptor(s).
R, elytral ridge.
RFM, rim-fold margin.
S, prosternum.
S2, mesosternum.
S3, metasternum.
SL, sternellum.
SPj, sternal projection.
Tn, trochantin.
Tn-RFM, trochantinal rim-fold margin.
ZF, zone of fusion between pleuron and trochantin.



Figures 1–12. Archostemata, Adephaga. 1. *Priacma serrata*. 2. *Cupes concolor*. 3. *Tetraphalerus wagneri*. 4. *Omma stanleyi*. 5. *Micromalthus debilis*. 6. *Agabus striatus*. 7. *Amphizoa insolens*. 8. *Carabus nemoralis*. 9. *Clivina impressifrons*. 10. *Metrius contractus*. 11. *Ozaena elevata*. 12. *Paussus* sp.

enclosed within the prothorax. Cervical sclerites absent, though proprioreceptors are present in the cervical membrane. Sternal flange with two long internal expansions that project ventrally and fuse with the ventral sternal wall near the midline, e.g., *Metrius*, *Clivina* (Figs. 157, 9, EndFL). In *Amphizoa* (Fig. 7) the internal part of the flange is small and does not reach the sternum.

Notum low, relatively inconspicuous in lateral view even in high volume forms, e.g., *Clivina* (Fig. 9). Lateral margin usually small and only slightly expanded, sometimes absent (*Apotomus*, *Tricondyla*, *Agra*), large and flattened only in *Sphallomorpha* and *Adelotopus* where it probably covers all movements of the proleg. Dorsal midline frequently bears a slender groove which represents the invagination crease of an internal carina. Transverse grooves or depressions near either or both the anterior and posterior margins of the dorsal surface may be present and represent zones of fusion of the anterior and posterior flanges to the notal wall.

Anterior pleural fold present though reduced and internal. In all *Adephaga* examined, the anterior sternal and notal flanges are joined via membrane (*Omus*) or via membrane and a dorsally directed sternal lobe, *Amphizoa*, or by fusion. The anterior pleural rim-fold is in all cases covered by the sternal flange. Membrane from the pleural invagination first joins the notal and sternal flanges and then runs into cervical membrane. The pleuron contributes neither cervical membrane nor a sclerotized surface to support the head. Externally, the notum and sternum are developed in front of the apex of the pleural fold and may be slightly separated (*Nebria*), meet edge on (*Carabus*, *Amphizoa*), overlap (*Ozaena*), or be tightly to solidly connected (*Clivina*, *Galeritula*, *Lebia*, *Helluomorphoides*). The anterior configuration of the Adephaga is similar to that of *Omma* and *Tetraphalerus* (Hlavac, 1972, figs. 11–14).

Pleuron large, rigid, forms a conspicuous part of the lateral body wall, rigidly attached to the notum and sternum. Notopleural joint long, usually membranous, sometimes solidly fused (*Agra*, *Tricondyla*) always enclosed by edge-on meeting of notal and pleural rims.

Endopleuron broad, usually developed dorsally to come quite close to the dorsal notal wall but is separated from it by the *notopleuralis* muscle, e.g., *Amphizoa* (Hlavac, 1972, fig. 9); sometimes it is fused to the notal wall in which case the *notopleuralis* is absent (e.g., *Agra*, *Tricondyla*, *Galeritula*). Commonly, this muscle consists of very short, widely-spaced fibers, that are most densely distributed anteriorly and posteriorly. The function of the *notopleuralis* is obscure. If the origin and insertion are both rigid, as seems to be the case, then contraction of this muscle can have no mechanical effect. On the other hand, if the endopleuron is subject to ventral bending as the muscles originating on its ventral surface contract, then contraction or the mere presence of this muscle could counter this force. Pleural rim-folds specialized relative to those of the Myxophaga and most Archostemata. Ventral rim-fold not distinct, modified anteriorly into a rigid carinate pleurosternal joint and posteriorly into a complex coxal housing. The pleurosternal suture marks an invagination crease and varies from nearly vertical (*Agabus*, Fig. 6) to nearly horizontal (*Clivina*, Fig. 9), it is sometimes absent.

Trochantinal and coxal articulation folds of sternum and pleuron are broad and form cowlings which enclose the coxal articular region and the trochantin. The cowlings either meet edge-on or the sternal rim slightly overlaps the notal rim. Posteriorly, the pleural fold is fused to the lateral pleural wall. It bears along its rim a ventrally projecting condyle that is inserted into a groove on the coxa to form the pleurocoxal articulation (Fig. 142).

Posterior pleural fold may be evaginated ventrally to form a projection which may be joined, in one of 3 ways, to the sternal

projection to form a complete collar or set of closed coxal cavities: it may overlap (*Ozaena, Metrius*, Fig. 157); enclose the pleural tip into sternal groove or cavity (*Clivina, Helluomorphoides*, Figs. 153–154) or enclose the sternal tip into cavity on pleural apex, e.g., *Omophron* (Bell, 1967, fig. 17). The projection may be short with a free apex (*Carabus*, Figs. 8, 149 PLPj) or the projection may be absent (*Agabus, Amphizoa,* Figs. 6–7). Dorsally, the posterior pleural fold forms a long flange that is always fused, near its inner margin, to the pleural wall.

The region of fusion of the ventral fold above the coxa, and of the posterior fold to the pleural wall is sometimes marked by a suturelike groove similar in cross section to the notal invagination crease-flange assemblies. This groove has been erroneously called the pleural suture (apophysis) by many authors who use it as a landmark to divide the pleuron into an anterior episternum and a posterior epimeron, but who do not attempt to explain its origin off the pleurosternal suture. A pleural suture and a proepimeron do not occur in the prothorax of the Coleoptera and are present in only a few Holometabola (Hlavac, 1972: 134–139).

Posterior to the endopleural invagination the notopleural joint varies from tightly membranous to solidly fused. In *Metrius, Rhysodes* and *Amphizoa* (Fig. 7) the rims of the notum and pleuron meet edge-on and are readily separated in a KOH'd specimen. The membrane from the pleural invagination curves medially and joins the intersegmental membrane. In many forms a small (*Trachypachus*) or large (*Carabus, Zacotus*) ventral lobelike expansion of the notal flange increases the length of the membranous notopleural connection. Solid fusion of the notal and pleural flanges and their rims is found in some carabids (*Galeritula, Lebia, Helluomorphoides*).

Coxal articular region enclosed, always small, and less than .25 total length of coxa. The articular region is distinctly produced above the coxal foramen in some, e.g., *Amphizoa* (Fig. 142) while in most carabids with closed coxal cavities this region is greatly reduced and is developed little above the level of the coxal foramen, e.g., *Helluomorphoides* (Figs. 143, 153), see section on promesothoracic joint below. A groove on the dorsal surface of the articular region receives the pleural condyle to form the pleurocoxal articulation (Fig. 142 PLCnd). In most Adephaga, a peg on the coxa is inserted into a cavity on the cryptosternum to form a sternocoxal articulation (Figs. 142–143) which restricts coxal motion to rotation. The sternocoxal articulation is absent but coxal flexation does not seem possible in the Gyrinidae, Dytiscini and Laccophilini and in the paussines (Evans, 1965). Proprioreceptors are present near the pleurocoxal articulation and near the trochantinocoxal joint (Fig. 143, PR).

Trochantin small (Figs. 142, 143, Tn), enclosed except in some forms, e.g., *Carabus* where a small section may be visible externally when the coxa is rotated far posteriorly. The trochantin is loosely attached to the sternum and pleuron but tightly joined to and moves freely with the coxa. The *nototrochantinalis* muscle serves as an accessory anterior coxal rotator.

Promesothoracic joint. The great structural and mechanical diversity in intersegmental attachment can be divided into two groups: (1) terrestrial forms (Caraboidea) with variable prothoracic mechanisms and (2) rigid body aquatic families plus *Omophron*.

Among caraboids, major differences are found in the completeness of the posterior collar and in the geometry of pro- and mesosternal articulation surfaces. Two major grades of development are recognized. The low grade mechanism of a few tribes is structurally uniform. The sternal projection extends behind and below the coxal apex, its articular surface is only slightly raised and is at a distinct angle to the narrow posterior margin of the intercoxal

septa, e.g., *Carabus* (Figs. 8, 149–152). The internal septa extends between the long coxae for only a short distance. The mesosternum is divided into a nearly vertical anterior region bearing a pair of concavities, sometimes separated by a median carina, that can receive the procoxae; and a ventral, horizontal, slightly concave posterior region that receives the dorsal surface of the prosternal projection. As the prothorax moves ventrally, the prosternal projection moves along the ventral surface of the mesosternum and the procoxae come to rest against the mesosternal concavities, blocking additional ventral motion. Dorsal movement of the prothorax increases the space between the coxae and mesosternum and results in the exposure of intersegmental membrane (Figs. 150–152).

A low grade ventral motility mechanism has been found in *Trachypachus, Systolosoma, Nebria, Leistus, Hiletus, Opisthius, Carabus, Calosoma, Ceroglossus* and in *Sphaeroderus*. All of these forms have open coxal cavities. Poorly developed though probably fully functional postcoxal bridges occur in the trachypachidines, *Leistus* and *Carabus*; in *Hiletus* the bridge is broad and heavily sclerotized.

The high grade ventral motility mechanism can be derived from a configuration similar to that of *Carabus* by performing four operations:

(1) Developing the sternal projection dorsally above the level of the coxal apex, broadening its articular surface.
(2) Developing the intercoxal septa dorsally and expanding it laterally over the median curvature of the coxa so that a broad surface is formed that curves posteroventrally from the apophysis and is continuous with the projection flange (Figs. 149, 153, 157).
(3) Reducing the length of the coxae, especially the articular region.
(4) Remolding the anterior part of the mesosternum to form an enclosable, slightly curving, nearly horizontal surface distinctly above the plane of the mesosternum proper.

This mechanism is an improvement over the low grade type in two respects. Since the pro- and mesosternal articular surfaces are above the most ventral sections of the pro- and mesosternum, there is a large ventral clearance permitting extensive ventral motion of the prothorax. Secondly, there is a broad overlap of pro- and mesosternal surfaces; dorsal movement of the prothorax will not expose ventral intersegmental membrane (Figs. 152, 156).

The high grade mechanism occurs, with significant variation, in many tribes of Carabidae and is associated with closed coxal cavities, except in *Gehringia*.

Of the forms examined, *Mystropomus* and *Metrius* (Figs. 10, 157) are the least modified over the low grade type. The coxae of *Metrius* are long (L/W 1.7), the intercoxal septa is not expanded and is much narrower than the relatively low articular surface of the projection.

As the flange is developed dorsally, and the internal septum expanded laterally while the coxae are reduced in length, the length of the actual articular surface is increased from simply that of the projection proper to the combined lengths of the projection and the septum. As these changes are occurring, an increasingly smaller amount of the coxa is visible in posterior view (Figs. 153, 157). The amount of coxa visible in posterior view between the pleural and sternal flanges is a measure of the development of the ventral motility mechanism. This varies from a large amount of coxal exposure, though less than in *Metrius* in some forms examined belonging to Sloane's "Carabidae clausae" and "Carabidae uniperforatae" (*Ozaena, Psydrus, Nomius, Promecognathus, Loricera, Rhysodes*), to little coxal exposure, similar to *Clivina*, in others (*Pterostichus, Zacotus, Ega*).

The least amount of coxa is visible in certain forms with a broad flangelike post-

coxal bridge. In *Helluomorphoides* (Figs. 153–156), for example, the pleural projection is broadened ventrally and the flange is developed anteriorly over the coxa. The ventral surface of the pleural flange is approximately coplanar with that of the sternal flange. The postcoxal bridge itself is slender and separates pericoxal from intersegmental membrane (Fig. 153, CxBr). The cavity between the pleural and sternal projections and the postcoxal bridge is the second foramen of the "biperforate" cavity of Sloane (1923). This foramen is large in some (*Agra*, *Lebia*, *Pentagonica* and *Omus*), but much smaller in others (*Anthia*, *Apotomus*, *Pangaeur*, and *Helluomorphoides*), and secondarily lost in *Sphallomorpha*.

In *Omophron*, the prosternal projection is long, broad and flattened. It rests on and completely covers the mesosternum; the intercoxal septum is not expanded over the coxae and is at a distinct angle to the projection. Large mesosternal concavities house part of the procoxae. A median groove on the projection receives a ridge on the mesosternum forming a ventral interlocking mechanism. A dorsal mechanism is formed from a pair of ridges on the elytra inserted into paired grooves on the notal flange. The pleural projection is developed laterad of the coxae and joined with the sternal projection. The prothorax is not moved as these beetles dig, rather the entire oval dorsal surface of the body is used to push and compress substrate. The prothorax is not moved during walking or running.

Omophron, then, is a rigid-body form with a ventral mechanism similar to that of the low grade forms described above. The combination of closed coxal cavities and mesosternal housing of the procoxae suggests that closed coxal cavities originated or have shifted function to increase the integrity of the already rigid joint by increasing the surface area of intersegmental overlap. A similar configuration is found in the curious African cicindeline *Platychila*.

The aquatic Adephaga, like most other aquatic Coleoptera, are rigid-body forms; their ventral motility mechanism can be derived from the low grade type of carabids. The ventral intersegmental connection of *Amphizoa* (Figs. 7, 158), differs little from that of *Carabus* (Figs. 8, 151). In *Agabus* (Fig. 6) the prosternal projection is divided into a thick, anterior portion that fits into a deep cavity on the mesosternum and a thin, tapering, posterior section that is placed in a metasternal groove. The promesothoracic interlocking mechanism of *Peltodytes* and *Haliplus* is extremely complex. The long, broad, prosternal projection bears a pair of anterior cavities that receive expansions of the mesosternum, and a posterior condyle that is placed in a metasternal cavity. In *Dineutes* and *Gyrinus* the prosternal projection consists only of an internal septum, the mesosternum is developed anteriorly between the coxae, the perpendicular edges of the mesosternum and projection meet edge-on. A thick, heavily sclerotized, postcoxal bridge is present in all aquatic Adephaga.

Bell (1966) concluded that the Haliplidae, Gyrinidae and the dytiscoid families represent three independent invasions of the aquatic zone. This conclusion was based in part on the assumption that open coxa cavities and postcoxal bridges occur together only in the aquatic Adephaga and trachypachidines. However, postcoxal bridges occur with open coxal cavities in *Hiletus*, *Leistus* and *Carabus*.

A postcoxal bridge is present in many Adephaga; it is formed from sclerotization of intersegmental membrane between slight expansions of the pleural flange and the sternellum (Figs. 153, 157, 158, CxBr, SL). In some carabids the postcoxal bridge is thicker but may not be more heavily sclerotized than the surrounding intersegmental membrane, e.g., *Metrius*, the ozaenines examined, possibly *Gehringia* as well as *Carabus*, *Notiophilus*, *Leistus*, *Scarites*, *Morion*, *Terehus*, some *Bembidion*, *Trachypachus* and *Systolosoma*. In these forms it

may be difficult to see the bridge after treatment with KOH. In the cicindelines examined, in the aquatic families and in *Hiletus* the bridge is thick and heavily sclerotized while in the tribes included in Sloane's "Carabidae Biperforatae" it is variable though always quite distinct.

Even an only slightly developed postcoxal bridge is probably effective in isolating pericoxal membrane from the effects of forces generated by prothoracic movement.

Paussines: Paussid beetles are myrmecophiles; most have prothoracic trichomes (Darlington, 1950:57–58). In many advanced paussids a pair of trichomes is located on the lateral margin of the notum and is joined by a deep transverse cleft or groove (Fig. 12). The development of these organs has caused many modifications of prothoracic structure, including: (1) Extensive development of the prothorax posterior to the coxa to house the trichome glands (compare *Ozaena*, Fig. 11, with *Paussus*, Fig. 12). (2) Reduction of the prothorax, including the endopleuron, anterior to the coxa. (3) Posterior development and fusion of the pleural projections to one another.

In the primitive paussids the prothorax is not developed posteriorly, the notopleural suture extends the full length of the prothorax and the pleural projections overlap the sternal projection as in *Ozaena*, e.g., *Protopaussus*, *Megalopaussus*, *Caribodomemmus*, *Arthropterus*, and some species of *Homopterus*. In *Homopterus bolivianus* Kolbe the pleural projections are slightly developed and fused posterior to the sternal projection.

Suborder **MYXOPHAGA**
Figures 13–16, 120–122

Pleuron variable in size, rigid, forms part of body wall; fused to trochantin. Anterior pleural flange external or enclosed.

Head prognathous, cervical sclerites absent.

Notum encloses a very low volume in *Hydroscapha* and *Sphaerius*, somewhat larger in *Lepicerus* where it bears a pair of anterolateral cavities that house the antennal club, and in *Hintonia* (= Ptyopteryx) where it bears a complex of interlocking devices on the posterior face.

In *Lepicerus*, *Hydroscapha* and *Sphaerius* the small anterior pleural flange is visible externally (Figs. 13–16). In *Hintonia* (Fig. 16) the notum and sternum and their flanges are developed anterior to the apex of the pleuron. The rim of the notum is housed in a cavity on the broad dorsal sternal face, and this region of overlap encloses the pleural flange. Internally, cervical membrane originates from the pleural flange as in other Myxophaga.

Pleuron apparently incapable of motion, joined broadly to notum via membrane slightly above the notal rim so that a small amount of the pleuron as well as the actual notopleural joint are both concealed. Endopleuron with ventral surface broadly concave in *Lepicerus* and *Hintonia*; however in *Hydroscapha* it is concave basally but compressed, flattened apically into a long horizontal region that is seen highly foreshortened in Fig. 121. The endopleuron of *Sphaerius* is strongly compressed from the base to the apex and is nearly horizontal and triangular in outline (Figs. 120–122).

Pleuron largest in *Hydroscapha*, comparatively reduced in *Hintonia* (Figs. 120–122). The anterior pleural fold includes the pleural flange in front of the cervical membrane and a small (*Lepicerus*) or large (*Sphaerius*) internal region behind it (Fig. 122, AFL, RFM). The ventral portion of the rim-fold includes the small inclined sternal attachment region above the trochantin and the coxal articulation behind it. Coxal fold broad or narrow and peninsulalike in *Hintonia*, encloses a small part of the articular region, except in *Hydroscapha*, where it is developed anteriorly to enclose most of the articular region. A tall and broad posterior pleural

flange is present in *Lepicerus*, in *Hydroscapha* it is tall and narrow.

The trochantin is solidly fused to the pleuron; there is no trace of either a suture, paired rim-folds or an internal zone of fusion.

Pleurosternal and trochantinosternal joints both membranous.

The sternum of *Hydroscapha* and *Sphaerius* is not folded extensively while that of *Lepicerus* and *Hintonia* is more structurally complex. Exosternum narrow, except *Hintonia*, reaches coxal apex or extends slightly below it. Sternal projection very small and acts as coxal separator in *Hydroscapha* where it arises from the cryptosternum, and in *Sphaerius* where it originates from the sternum and extends in front of the anterior sternal margin. Projection large in *Lepicerus* and *Hintonia* where it extends below and behind the coxae.

Sternacostal suture distinct in *Sphaerius* but in *Hydroscapha* it runs alongside of and may be confused with a slight fold that separates a concave, anterior region (housing the coxa) from a convex, posterior region (including most of the horizontal sternellum). In *Lepicerus* and *Hintonia* the sternellum is smaller and vertical.

In *Lepicerus* and *Hydroscapha* the cryptosternum and the inner face of the pleuron come quite close together, overlap slightly, or may actually touch. Pericoxal membrane is then either completely separated from intersegmental membrane, forming dorsal closure of the coxal cavities, or there may be only a slight region of continuity between the two membranous regions.

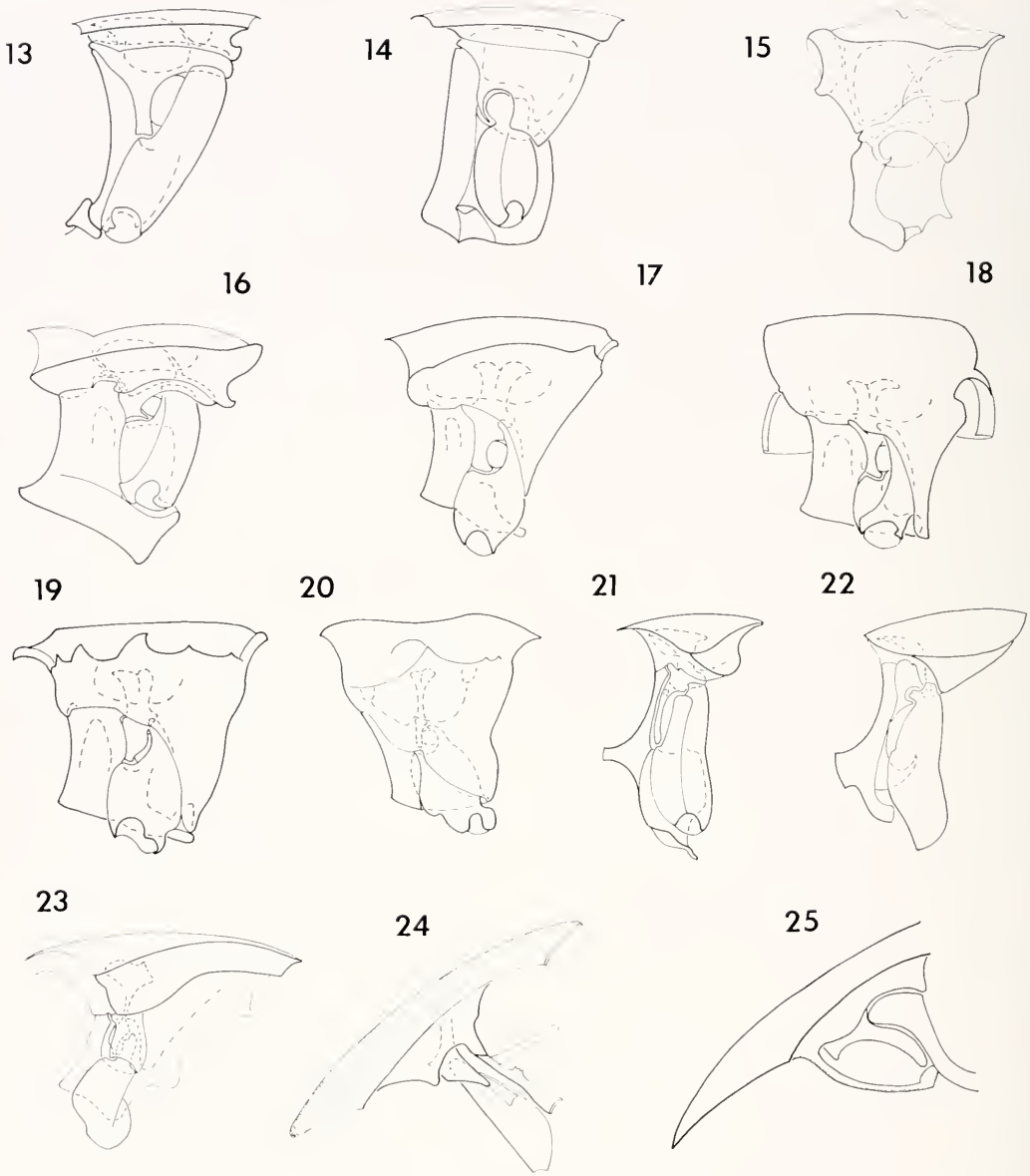
Coxal articular region varies from .3 (*Sphaerius*), to about .2 (total coxal length in the other genera). Coxa elongate to squat, in *Lepicerus* a ridge on the coxa near the apex articulates with a groove in the endosternum. The very broad posterior notal and pleural flanges suggest that Myxophaga are rigid-body forms.

A promesothoracic interlocking mechanism is present only in *Hintonia*. The notum bears a small posterior wall, its ventral margin is expanded into a small carina that is inserted into a groove on the anterior elytral face. Medially, the notum is arched dorsally and the flange fits against the broad, similarly folded mesonotum. The posterior dorsal margin bears a single crenulation which fits against the scutellum. Laterally, the notal flange becomes very broad and rests on the tomentose dorsal surface of the mesepisternum. The very small notal projection probably rests on a slight shelf on the lateral face of mesepisternum. The broad sternal projection extends behind the coxae and rests on the mesosternum; a condyle on the anterior margin of the sternum is inserted into a cavity on the sternal projection. The procoxae are partially housed in small cavities on the anterior face of the mesosternum.

The broad flattened profemora of *Sphaerius* can be brought to lie flush against the mesosternum. In addition, its inner surface has a long cavity that houses the protibia.

Suborder **POLYPHAGA**

Pleuron greatly reduced in length and width relative to that of other suborders, varies from largely external to completely enclosed by notal or sternal cowlings or both; may be motile but is never an element of the body wall. Reduction most evident in the external region which extends from the notal rim to the trochantin (e.g., Fig. 128 PL, stippled portion). This section is largest in certain primitive taxa (Eucinetoidea, Staphylindidea, Derodontoidea) and may be much wider than the trochantin (Figs. 17–22, 123–128). A result of pleural reduction is the enclosure of the dorsal aspect of the pleurocoxal articulation by notal rim-folds. An anterior pleural fold, formed from an evaginated ventral pleural rim-fold is present in some members of the same primitive groups and inserts between the notum and sternum; this



Figures 13–25. Myxophaga, Derodontoidea, Eucinetoidea. 13. *Sphaerius politus*. 14. *Hydroscapha natans*. 15. *Lepicerus horni*. 16. *Hintonia britskii*. 17. *Laricobius rubidus*. 18. *Peltastica tuberculata*. 10. *Derodontus maculatus*. 20. *Nothoderodontus gourlayi*. 21. *Prionocyphon lembatus*. 22. *Eucinetus infumatus*. 23. Undescribed Clambid. 24. *Clambus gibbosus*. 25. *Loricaster* sp.

structure is homologous with the anterior flange of Archostemata and Myxophaga (Figs. 1, 122, 123, 125, AFL; Hlavac, 1972, figs. 10–18). The enclosed region of the pleuron, between the notal rim and the endopleural invagination, highly variable in size and sensitive to pleurocoxal mechanics (Figs. 123–134, area between dotted

line and notopleural membrane). Endopleuron quite variable in height relative to that of the notum and in degree of basal compression and apical expansion (Figs. 123–136 EndPL).

Pleuron and trochantin fused. Boundary between these sclerites present internally in only a few groups and indicates joining of rim-fold surfaces (Figs. 123, 124, 128 ZF). Pleural and trochantral rim-folds and a zone of fusion are absent in most Polyphaga and all Myxophaga which prevents accurate determination of the site of attachment.

For purposes of terminology the trochantinopleural boundary is taken to be at the level of the most ventral point of a distinct dorsal coxal articulation. Trochantin and coxal articular region vary greatly in relative size (Figs. 135, 136, 144–148 Artic) and may be almost completely exposed (Figs. 19, 21, 22, 42–44, 53–55, 89–97, 99–104, 111–119) or wholly enclosed (Figs. 20, 56–66, 80–84, 106–109).

The pleuron, endopleuron and trochantin may be motile and function to aid coxal rotation or cause coxal flexation via a lever mechanism with the region of the pleuron just below the invagination serving as a fulcrum (e.g., Figs. 53–54, 132–133). In many cases the pleuron is rigidly fused to the notum and the endopleuron may be fused to the notal wall.

Notum and sternum, while joined primitively by membranous rim-fold joints, are often solidly fused together and in some cases the notosternal suture is absent.

EUCINETOIDEA
Figures 21–25, 123, 125, 126, 166

Very small, low volume prothoraces, part of a variable compaction mechanism. Pleuron rigid, large externally, may bear a small anterior fold and a zone of fusion to the trochantin. Coxae elongate, external; sternum thin.

Head in rest position hypognathous to opisthognathous; its posterior face is flattened and lies flush against either the procoxae, mesosternum or metasternum, partially to wholly concealing the proleg. One or two cervical sclerites present.

Notum small with very large flattened lateral margins in clambids. Notal projection absent, except in *Loricaster* (Fig. 25), where it is fused with and does not extend below the cryptosternum.

Thin lateral arms of sternum attached via membrane to notum, above coxal articulation. Without sternal projection but with large sternellum and distinct basicostal suture as well as an intersegmental sclerite bearing a spinasternum in *Clambus*, or with a broad cryptosternum in *Loricaster*. In eucinetids and helodids, there is no intersegmental sclerite and the sternum is evaginated medially to form a projection. Sternellar projection small, fused with sternal projection.

Pleuron immovable, joined to notum near rim with large external component above coxal articulation and with anterior fold. In *Sarabandus* (Fig. 123) pleural and trochantinal rim-folds are present as well as a distinct zone of fusion between these sclerites. Fusion zone almost entirely obliterated in *Prionocyphon* (Figs. 21, 25). In the eucinetids and clambids only the pleural rim-fold is present (Figs. 22, 126).

Trochantinocoxal articulation normal, except in *Eucinetus* where it is quite compressed. Pleurocoxal articulation large. Coxae long and narrow, usually entirely external, with a slight articulation against unfolded notal rim.

Promesothoracic interlocking mechanism similar in eucinetids and helodids. Lateral rim of notum rests on the infolded mesepisternum. Anterior faces of mesosternum and episternum concave, partially house procoxae. Medial mesosternal fossa receives apex of the prosternal projection.

In *Clambus* a dorsal interlocking mechanism consists of three mesothoracic elements: the rim of the scutum, an episternal condyle, and an elytral carina, that fits into an elongate groove on the posterior notal flange.

Eucinetoids are moderately to very highly

compacted beetles. A measure of compaction is the number of appendages enclosed in rest position. In helodids, the anterodorsal face of the procoxa is hidden by the head while the posterior coxal face is only slightly enclosed by mesosternal cavities. In eucinetids only a slender lateral section of the procoxae is visible, between the head and the mesothorax. In both groups, the lateral margin of the pronotum is not expanded.

There is considerable variation in the compaction mechanisms of clambids. All, however, have large, flat lateral prothoracic margins. In *Loricaster* the mesosternum is inflected dorsally. The entire proleg is enclosable within a cavity formed by the margins of the head and pronotum resting against the elytra and mesothorax. The flat mesofemur is external. The tibia and tarsi are housed under it. In *Clambus, Sphaerothorax*, the anterior part of the metasternum is also inflected dorsally, the anterior margin of the head then rests against the metasternum enclosing both the pro- and mesolegs. In *Calyptomerus* the anterior margin of the head rests on the metathorax and the pro- and mesoleg are enclosed (Fig. 166). In each of these genera, the anterior margin of the head rests on a pterothoracic sternite, forming, along with the pronotal margins, a cavity that can completely enclose the proleg and sometimes the mesoleg as well.

The flat surfaces of the mesosternum and most of the metasternum are inflected far dorsally above the ventral plane in *Clambus, Sphaerothorax,* and *Calyptomerus* (Fig. 166). The flat ventral surface of the head and the prothorax rest against these inflected surfaces and can completely enclose the thin, poorly sclerotized pro- and mesolegs.

In *Loricaster* the posterior notal flange bears a small posterior wall. Bearing a groove that houses an elytral carina. Mesosternum inflected dorsally nearly 90° from ventral plane of the metasternum. Proleg and mesocoxa poorly sclerotized and can be enclosed. Mesofemur sclerotized and flat, exposed and can conceal tibia and tarsus under it when animal is compacted.

An undescribed genus (Fig. 23), known from Micronesia and the West Indies, differs from other eucinetoids in many characters: (1) The notum is produced below the level of the notosternal joint enclosing most of the trochantin and coxal articular region. (2) The pleuron lacks an anterior fold and is without a large external component. (3) Endopleuron with slender stalklike base and expanded apex. (4) Cryptosternum is fused to the notal projection. (5) The coxa is differentiated into a narrow apical region enclosed within the notum and a squat external portion. (6) The compacting mechanism does not involve the head's resting against the meso- or metasternum enclosing at least the proleg as in other clambids. The mesosternum is, however, inflected approximately 45° and bears a pair of concave regions, separated by a carina, for reception of the posterior faces of the procoxae. The head covers only the anterior coxal face; cavities under the notal margin house, but do not enclose, the antennal apex and part of the leg.

The prothorax of this form can be derived from that of other eucinetoids by employing common transformations, e.g., enclosure of coxae and differentiation of the endopleuron. The inflected mesosternum could indicate derivation from a form with a *Clambus*- or *Loricaster*-like compaction mechanism.

DERODONTOIDEA

Figures 17–20, 127

Low volume configurations with closed coxal cavities except *Laricobius*, and with deep coxal enclosure in *Nothoderodontus*. Pleuron rigid, usually bears a large anterior fold. Pleural and trochantinal rim-folds and zone of fusion between them are all absent.

Head prognathous, deeply inserted within prothorax. The single cervical sclerite is enclosed.

Lateral rim of notum expanded and flattened (*Peltastica*, Fig. 18) or less developed but with toothed margin (*Derodontus*, *Nothoderodontus*, Figs. 19, 20) or not expanded and without serrate margin (*Laricobius*, Fig. 17). Projection broad, reaches sternal projection except in *Laricobius*.

Notosternal joint membranous. Cryptosternum with concavity for reception of anterior face of trochantin and for housing the anterior pleural fold.

Pleuron immovable, joined to notum near rim, except *Nothoderodontus* where extensive dorsal development of the notal rim-fold results in enclosure of the entire coxal articular region. Endopleuron with longitudinal crease forming a ventral carina. Anterior pleural fold large, distinct externally in *Peltastica* and *Laricobius* (Fig. 127), smaller and enclosed in *Derodontus*, absent in *Nothoderodontus*. Pleural and trochantinal rim-folds and zone of fusion are absent or very obscure. Anterior face of trochantin large, housed within concavity in cryptosternum. Small portion of articular region and part of posterior face of the squat coxa housed within notum except in *Nothoderodontus* where anterior expansion of the ventral portion of the notal projection encloses the lateral coxal face (Fig. 20). Coxae extend below level of sternal projection. Pleurocoxal articulation compressed, with strong groove-ridge device.

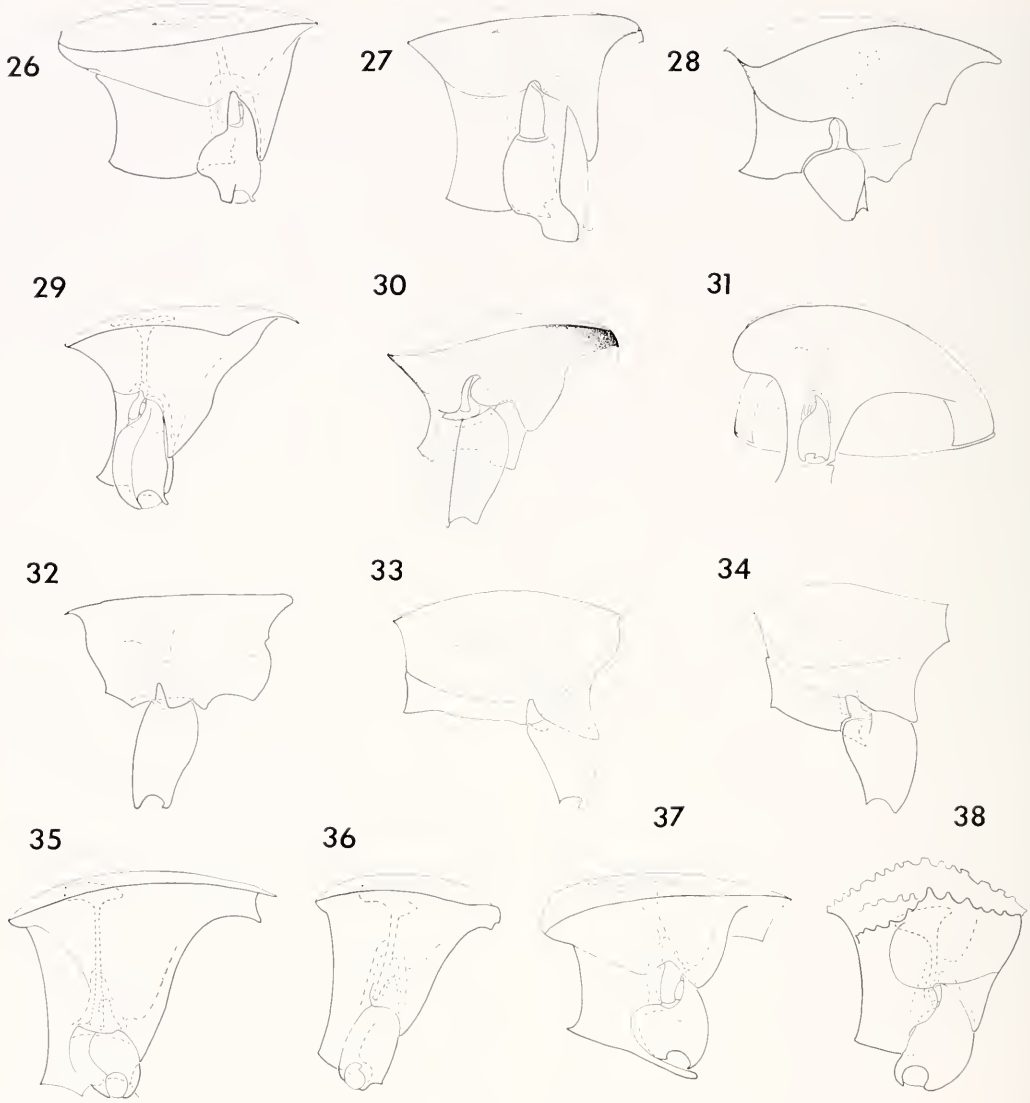
Apices of notal and sternal projections overlap, though are not tightly fused in *Peltastica* and *Derodontus*, forming a complete articulation collar and closed coxal cavities. In *Laricobius* the notal projection is separated from the sternal projection (Fig. 17); a groove in the mesosternum and two concave regions house the prosternal projection and part of the procoxae respectively.

STAPHYLINOIDEA

The immense prothoracic diversity of staphylinoids has resulted from multiple, variably parallel transformations of a primitive/generalized polyphagous prothorax. Similar generalized configurations are found in each of three major lineages: Leiodidae (*Catopocerus*, *Hydnodbius*, Figs. 26–27); Silphidae (*Lyrosoma*, *Necrophilus*, Figs. 39–40); and Staphylinidae (*Omalium*, *Trigonurus*, Figs. 45, 46). Unspecialized forms with reduced coxal articular regions include: *Leptinillus*, *Micropeplus*, *Dasycerus*, and the hydraenids (Figs. 37–38, 67–70). Divergence from this sort of stem array has taken several pathways, leading to forms capable of extensive coxal flexation as well as those with deep enclosure of long and squat coxal articular regions. The latter cases may also be associated with specialized pleurocoxal mechanisms.

Different mechanisms permitting large scale coxal flexation have evolved in the Leiodidae (*Prionochaeta*, Fig. 30), Silphidae (*Necrodes*, Fig. 42); and in the Staphylinidae (*Philonthus*, Fig. 54). Extensive enclosure of elongate coxal articular regions is found in several taxa: Staphylinidae (*Stenus*, *Bledius*, *Leptochirus*, Figs. 56, 57, 51); Pselaphidae (*Sonoma*, Fig. 61); Scydmaenidae (*Clidicus*, Fig. 62). Enclosure of a relatively squat coxa and loss of pleural motility is found in Ptiliidae (Figs. 35–36) and some Scaphidiidae (*Scaphisoma*, Fig. 60), and a few scydmaenids (*Connophron*, Fig. 66).

Reduction of the length and width of the sternum as part of a compaction system or as an element of a flexation mechanism or both can be found in the Leiodidae (Figs. 28–30, 32); Silphidae (Figs. 39–42); Staphylinidae (Figs. 54–55); Scaphidiidae (Figs. 59–60); Scydmaenidae (Figs. 61–63); Pselaphidae (Figs. 64–66). Ventral closure of the coxal cavities is uncommon but found in *Leptochirus* and *Hydraena* (Figs. 51, 70), an elongate notal projection extending far below the trochantin is more widely distributed (Figs. 26–27, 39–40, 45–48). Dorsal closure common (Figs. 29–31, 35, 61, 69). The extensive variation within most families is considered at length below.



Figures 26–38. Staphylinoidea. 26. *Catopocerus* sp. 27. *Hydnobius matthewsi*. 28. *Camiarus* sp. 29. *Anisotoma polita*. 30. *Prionochaeta opaca*. 31. *Agathidium* sp. 32. *Astagobius angustatus*. 33. *Glacicavicola bathyscioides*. 34. *Brathinus nitidus*. 35. *Acratrichis* sp. 36. *Nossidium* sp. 37. *Leptinillus valious*. 38. *Dasycerus carolinensis*.

LEIODIDAE

Figures 26–33, 131, 163, 165

The diversity of prothoracic configurations and pleurocoxal mechanisms within the leiodids examined can be divided into four groups.

(1) Generalized high volume forms with open coxal cavities, where the notal projection is a bar to coxal flexation, e.g., *Catopocerus*, *Hydnobius* (Figs. 26, 27).

(2) Anteriorly compacted forms with reduced sterna and dorsally closed

coxal cavities which prevent coxal flexation, sometimes with a leg enclosure mechanism, e.g., *Anisotoma*, *Agathidium* (Figs. 29, 31).

(3) Compacted forms as in (2) but with partially to almost completely enclosed trochantins and with a complex of structural modifications to permit coxal flexation, e.g., *Prionochaeta* (Fig. 30).

(4) Uncompacted troglobitic forms with long legs, elongate prothoraces and with coxae capable of flexation, e.g., *Glacicavicola*, *Astagobius* (Figs. 32–33).

Description: Head-prothoracic joint variable; the forms studied can be divided into three groups. In *Hydnobius*, *Catopocerus*, *Camiarus* and *Neocamiarus*, the prognathous head is simply enclosed within the prothorax, the anterolateral region of the notum is not curved medially and the sternum is broad in front of the coxae. In *Colon* and *Platycholeus* the hypognathous head is also simply enclosed, but the sternum in front of the coxa is thin. The anterolateral region of the notum of *Anisotoma* and *Agathidium* curves medially, the hypognathous head rests against it and the thin sternum. In *Ptomaphagus*, *Catops*, *Nemadus* and *Prionochaeta* (Fig. 30) the notum is also curved medially and the sternum is narrow in front of the coxae. In addition, the posterior region of the head is divided into a distinct narrow neck, enclosed within the prothorax, and a large flat area which rests against the notum, sternum and coxae. Cervical sclerites always present.

Lateral margin of notum greatly expanded in *Agathidium* (Figs. 31, 165) as part of a clambid-like enclosure mechanism, less so in other leiodines, notum expanded only posteriorly in catopoids. In *Catopocerus* and in most species of *Hydnobius*, the notal projection is triangular in cross section, blocks coxal flexation posteriorly and is not connected to the sternum (Figs. 26, 27). The notal projection of *Anisotoma* and *Agathidium* is triangular in cross section and blocks coxal flexation, but the posterolateral edge of the sternum fits into slight groove on the inner face of the notum closing the coxal cavities dorsally. In the catopids, the notal projection is flat (not a barrier to coxal flexation) and is broadly joined to the sternum. There is variation in the posterior notosternal connection. In *Catops* and *Platycholeus*, the notum simply overlaps the sternum; while in *Prionochaeta* they must edge-on anteriorly and overlap posteriorly. In *Ptomaphagus* the entire joint is edge-on with a distinct suture; the suture is lost in *Colon*.

In *Catopocerus*, *Hydnobius*, and *Anisotoma* the notum, posterior to the coxae, curves, medially forming a cavity under the lateral margin for reception of the proleg. In catopoids, the notum above the coxae is curved outwards, but posteriorly it curves inwards and is entirely mesad of the coxae (Figs. 30, 163), and not a barrier to posterior coxal flexation. These curvatures are slightly developed in *Camiarus*. Notal rim-fold produced ventrally to form long condyle in *Catopocerus*, *Hydnobius*, *Agathidium*, and *Anisotoma*, which articulates with the coxa and pleuron.

Notosternal joint rigid, horizontal or nearly so, slightly inclined in *Catopocerus*, articulation folds distinct only in *Hydnobius*, suture absent in *Colon*.

The sternum extends well in front of coxae and the cryptosternum is slender in *Catopocerus*, *Hydnobius*, *Camiarus*, *Neocamiarus* (Figs. 26, 27). In *Agathidium* and *Anisotoma* (Figs. 31, 29) and in the other catopoid genera, the sternum does not extend far in front of the coxae (see head-prothorax joint above) and the cryptosternum is broad. Projection produced ventrally to form a small intercoxal septa.

Pleuron motile, attached to notum near rim except in *Platycholeus* and *Ptomaphagus*. Endopleuron with a long compressed base and an expanded apex in *Catopocerus* (Fig. 131); and with a squat base in *Ptomaphagus*; endopleuron intermediate in

other forms examined. Slender flat coxal articular face of trochantin folded approximately 90° from sternal face in *Catopocerus, Hydnobius*, and *Agathidium*. In the catopoids, the coxal face is distinctly concave and is capable of enclosing the entire coxal articular region. Only the trochantinal rim-fold is distinct in the genera examined.

Articular region of coxa small, less than .35 total coxal length, short and compressed in catopoids to form slender neck which fits into a trochantinal concavity (Fig. 147). Coxa extends below sternum, ranges from squat and small (*Catopocerus, Camiarus*) to elongate and very large (*Prionochaeta*). Coxal and trochantinal enclosure quite variable. In *Catopocerus, Hydnobius, Agathidium* and *Anisotoma* the notal and sternal cowlings are small, the pleuron articulates near the notal rim; only a small part of the trochantin and coxa are enclosed. In the catopoids, these cowlings are enlarged, do not overlap, there is always at least a small space between them; enclosure least developed in *Colon*, most so in *Ptomaphagus*.

The pronotum rests broadly on the mesonotum and elytra, while laterally the rim of the mesepisternum is slightly enclosed within the prothorax. In forms with dorsally closed coxal cavities the posterior sternal flange encloses the rim of the mesosternum. When the pronotum rests on the elytra and the mesothoracic rim is enclosed within the prothorax, little prothoracic motion seems possible (Fig. 163).

The procoxae of the catopoid genera are capable of flexing through a large angle. This is made possible through modifications of the sternum, notal curvature, and of the pleurocoxal articulation and its enclosure. The slender sternum is not only part of the compaction device but also permits the coxae to move further anteriorly than a broad sternum extending to the coxal apex. Posteriorly, the sternum curves inwardly, permitting posterior flexation.

In *Anisotoma* (Fig. 29) the notal projection is laterad of the inner coxal face; posterior coxal flexation is geometrically impossible. In the catopoids, closed coxal cavities are retained, coxal flexation is made possible by curving the notum and coxal articulation outwards anteriorly, and curving the notum sharply inwards posteriorly. These modifications bring the entire coxa laterad of the notal projection and permits a large angle of posterior flexation (Fig. 30).

Enclosure of the trochantin and coxal articular region is a general adaptive improvement that serves to project membrane connecting moving parts. Coxal and trochantinal enclosure in forms capable of flexation requires more internal space or smaller, more compact moving parts than would be required in forms capable only of coxal rotation. The trochantin and coxal articular region are sharply reduced in anisotomids capable of flexation. The amount of coxal enclosure is variable; sternal and notal cowlings almost completely enclose the coxae and trochantin in *Ptomaphagous*, less so in *Prionochaeta* and *Camiarus* (Figs. 28, 31). The coxal articular region is compressed into a small, slender neck (Fig. 147) and is enclosed within the concave articulation face of the trochantin.

Bathysciinae and *Glacicavicola*

The prothorax of many of the troglobitic bathysciines is elongate and nearly circular in cross section. However, their pleurocoxal mechanism is easily derivable from that of catopoids. In *Astagobius*, most of the slender coxal neck and trochantin are enclosed (Fig. 32). Posterior to the coxal articulation the notum and sternum are solidly joined and curve inwardly.

The prothorax of *Glacicavicola* (Fig. 33) is also elongate. However, it is developed in front of the coxae, with a long notosternal joint. The coxa and the trochantin are partially enclosed. The notal projection is large, extends laterad of the coxae, and covers a portion of it below the pleural articulation. Coxal flexation is possible

since the inner surface of the notal projection is flat. The coxae simply move under it as in some silphids. A pleurocoxal mechanism of this type is readily derived from that of a generalized staphylinoid (*Lyrosoma, Hydnobius, Catopocerus*).

SILPHIDAE
Figures 39–42, 129–130, 162

Generalized configurations with relatively high volume and coxae capable only of rotation, e.g., *Lyrosoma, Necrophilus* (Figs. 39–40) *or* variably reduced forms, with low enclosed volume and coxae capable of a high degree of flexation, e.g., *Nicrophorus, Necrodes* (Figs. 41–42).

Notum with large flat expanded margins in *Necrophilus* (Fig. 40), *Pelatines, Silpha* and *Necrodes* (Fig. 42). Notal projection acutely triangular in outline, reaches below trochantin and is triangular in cross section, blocking flexation in *Pteroloma, Lyrosoma, Pelatines*; long though not a bar to flexation in *Necrophilus*. Inner surface of the notal projection is flat, broad in outline, and reaches slightly above the trochantin in *Silpha*; projection is at level of trochantin in *Nicrophorus*, but in *Necrodes* it extends just below the dorsal pleurocoxal articulation.

Notosternal joint horizontal or nearly so, tightly membranous. Notal and sternal rim-folds present.

Sternum highly variable in horizontal and vertical development; the extremes are *Lyrosoma* and *Necrodes*. Sternal projection thin, acts as coxal separator, reduced in the silphines and nicrophorines.

Pleuron motile. Endopleuron with squat base and expanded apex in *Lyrosoma* (Fig. 129), *Pteroloma, Necrophilus* and *Pelatines*. However, in *Nicrophorus* (Fig. 130), *Silpha* and *Necrodes* it is expanded immediately above the apophysis. Exopleuron with anterior pleural fold that articulates with the sternum as well as with an external dorsal pleurocoxal articulation in *Necrophilus* and *Pelatines*. In other genera the posterodorsal edge of the sternum is inserted into a small cavity on the ventral surface of the pleural fold. Trochantin long folded lengthwise. Internally, a pleural rim-fold is present but does not extend far below the pleurocoxal articulation. Zone of fusion between pleural and trochantinal rim-folds usually present.

Coxa articular region large (.35–.56 coxal length). Coxae capable of flexation in forms with reduced or flat notal projections, e.g., *Nicrophorus, Necrodes*.

Promesothoracic joint variable. Mesosternal cavities for reception of procoxae present in *Pelatines, Necrophilus* and *Lyrosoma*.

Spiracular sclerites present, median sclerites present in *Silpha, Necrodes*, and *Nicrophorus*.

STAPHYLINIDAE
Figures 43–58, 124, 128, 132–133, 136, 144–146

The great diversity of prothoracic configurations within the staphylinids can be divided into three groups:

(A) *Generalized forms*. Coxal articular region long (about .30 total length) dorsal articulation normally enclosed. A main sequence array of configurations ranging from high volume forms with large nota and sterna, the latter extending close to the apex and far in front of the relatively small coxae, e.g., *Nodynus, Trigonurus, Omalium, Osorius* (Figs. 45–47, 50), to low volume forms with low nota and variable sterna, e.g., *Empelus, Proteinus, Tachinus* (Figs. 43–44, 49).

(B) *Forms capable of high coxal flexation*. Derivable from the generalized type by: 1. reducing the sternum so that it extends slightly in front of and just below the trochantin; 2. reducing both the height of the notum and the length of its projection; 3. increasing the length and width of the coxae while decreasing as well as enclosing the articular region. A continuous series probably exists betwen the forms capable of flexation and the highly modified forms included here, e.g., *Lathrobium, Philonthus, Aleochara* (Figs. 53–55).

Figures 39–52. Staphylinoidea. 39. *Lyrosoma opaca*. 40. *Necrophilus hydrophiloides*. 41. *Nicrophorus* sp. 42. *Necrodes surinamensis*. 43. *Empelus brunnipennis*. 44. *Protenus sulcatus*. 45. *Omalium marginatus*. 46. *Trigonurus crotchii*. 47. *Nodynus leucofasciatus*. 48. *Piestus* sp. 49. *Tachinus fimbriatus*. 50. *Osorius stipes*. 51. *Leptochirus* sp. 52. *Oxyporus lateralis*.

(C) *Forms with internalized coxae*. Derivable from the generalized type by enclosing the articular region of the coxa through: 1. dorsal growth of the notal cowling, e.g., *Piestus*, *Leptochirus* (Figs. 48, 51); 2. overlap and fusion of notal and sternal cowlings, e.g., *Stenus*, *Oxytelus*, *Bledius* (Figs. 56–58).

Description: Head prognathous in most forms, hypognathous in *Conosomus*, *Aleochara*, *Habrocerus* and in *Gymnusa*. Cervical sclerites present.

Height of notum and development of its lateral margins highly variable. Lateral margins expanded in *Megarthrus, Habrocerus, Tachinus*, and *Conosomus*, but much reduced in *Bledius, Stenus*, and *Oxyporus*, where the notum is ovoid in cross section.

Notal projection variable. Among the Proteininae the notal projection is small and broadly curved in *Proteinus* (Fig. 44), *Megarthrus* and in the genera figured by Steel (1969), except *Spiphotelus* and *Alloproteinus*, where it is long and triangular in outline. These two genera lack large spiracular sclerites. In the omaliines examined as well as in *Trigonurus, Siagonium, Oxyporus, Osorius, Pinophilus, Lathrobium* and *Tachinus* the notal projection is long, reaches the level of the trochantinal apex and is triangular in outline (Figs. 46, 52, 50, 53, 49). The projection extends below the trochantin in *Piestus* and *Leptochirus* (Figs. 48, 51); in the latter it is attached to the sternal projection. A short projection is present in *Bledius* (Fig. 58). In *Oxytelus* and *Stenus* the notum is developed far ventrally, its margin is horizontal (Figs. 57, 56). A thin, small notal projection distinctly less sclerotized than the surrounding regions occurs in *Creophilus*; the projection is absent in *Thinophinus* and *Philonthus* (Fig. 54). A small projection is present in *Xenodosa* but absent in *Aleochara* (Fig. 55). In *Conosomus* the short projection originates posterior to the coxa and articulates with the spiracular sclerites.

Membranous notosternal joint present in the omaliines and proteinines examined as well as in *Tachinus, Conosomus, Aleochara* and *Habrocerus*. Solid joint with distinct suture found in the piestines, osoriines and in *Oxyporus, Lathrobium* and *Pinophilus*; suture very faint in *Stenus* and *Philonthus*. Notosternal suture absent in *Bledius, Oxytelus*.

Ventral and anterior development of sternum varies from greatly reduced in *Philonthus* and *Aleochara* (Figs. 54, 55), where the notosternal joint is dorsad of the posterior notal margin and extends slightly below and not far in front of the trochantin; to well developed in high volume forms where it extends close to and far in front of the coxal apex, e.g., *Trigonurus, Leptochirus* (Figs. 46, 51). Sternal projection short, vertical, acts as a coxal separator in the proteinines, omaliines examined as well as in *Piestus, Trigonurus, Osorius, Oxyporus, Bledius, Stenus, Lathrobium* and *Pinophilus*. Sternal projection absent in *Tachinus, Habrocerus, Aleochara, Xenodusa* and the staphylinines examined. In *Leptochirus* (Fig. 51) a broad sternal projection extends behind the coxae and is united with the notal projections at the level of the coxal apex forming closed coxal cavities, its dorsal surface is enlarged posteriorly into a flange that articulates with the mesosternum. Dorsal surface of projection forms a flange in *Osorius*. Coxal cavities may also be closed by scleritization of intersegmental membrane that either includes the spiracles (*Pinophilus*) or does not (*Conosomus*).

Pleuron motile. Endopleuron with sharply constricted base and large expanded apex in *Trigonurus* (Fig. 46) though it is somewhat constricted and then expanded in *Oxyporus* and *Lispinus* (Fig. 52). In the other forms examined the endopleuron is not differentiated into a base and apex, its dorsal surface may be horizontal and ranges from slightly concave in *Empelus, Proteinus* and *Anthobium* (Figs. 43–44, 124) to highly concave, almost globose, in *Philonthus* and *Lathrobium* (Figs. 133, 132), or its surface may be flat and vertical as in *Piestus* (Fig. 48).

Trochantin and exopleuron highly variable, latter usually broad, pleurocoxal articulation is enclosed, except *Tachinus*. A small low anterior pleural fold may be present, but only in *Proteinus* (Fig. 128) and *Megarthrus* does it have a distinct articulation with the sternum. In forms where the trochantin is not enclosed, it may be folded lengthwise, usually nearly 90°, forming sternal and coxal attachment surfaces. However, in *Habrocerus, Xantholinus* and *Lathrobium* (Figs. 53, 133) the

trochantin is flat, almost folded back on itself, and is laterad of the sternum. The trochantin is flat and not folded lengthwise in forms where it is enclosed, e.g., *Oxytelus*, *Bledius*, *Stenus*. Internally, a pleural rim-fold is usually present, may be external and may extend far below the pleurocoxal articulation in forms with broad endopleura, e.g., *Omalium*, *Proteinus*, *Anthobium* and *Tachinus* (Figs. 45, 44, 128, 49, 128 PL stippled region). In forms with narrow endopleura the rim-fold is present but does not extend far below the dorsal coxal articulation, e.g., *Trigonurus*, *Oxyporus*. The pleural rim-fold appears to be absent in *Oxytelus*, *Bledius*, and *Stenus*. An external line of fusion in the solid zone between the pleural and trochantinal rim-folds is present only in *Tachinus* (Fig. 49). A zone of fusion between pleural and trochantinal rim-folds is usually visible internally (Figs. 124 A, B, ZF).

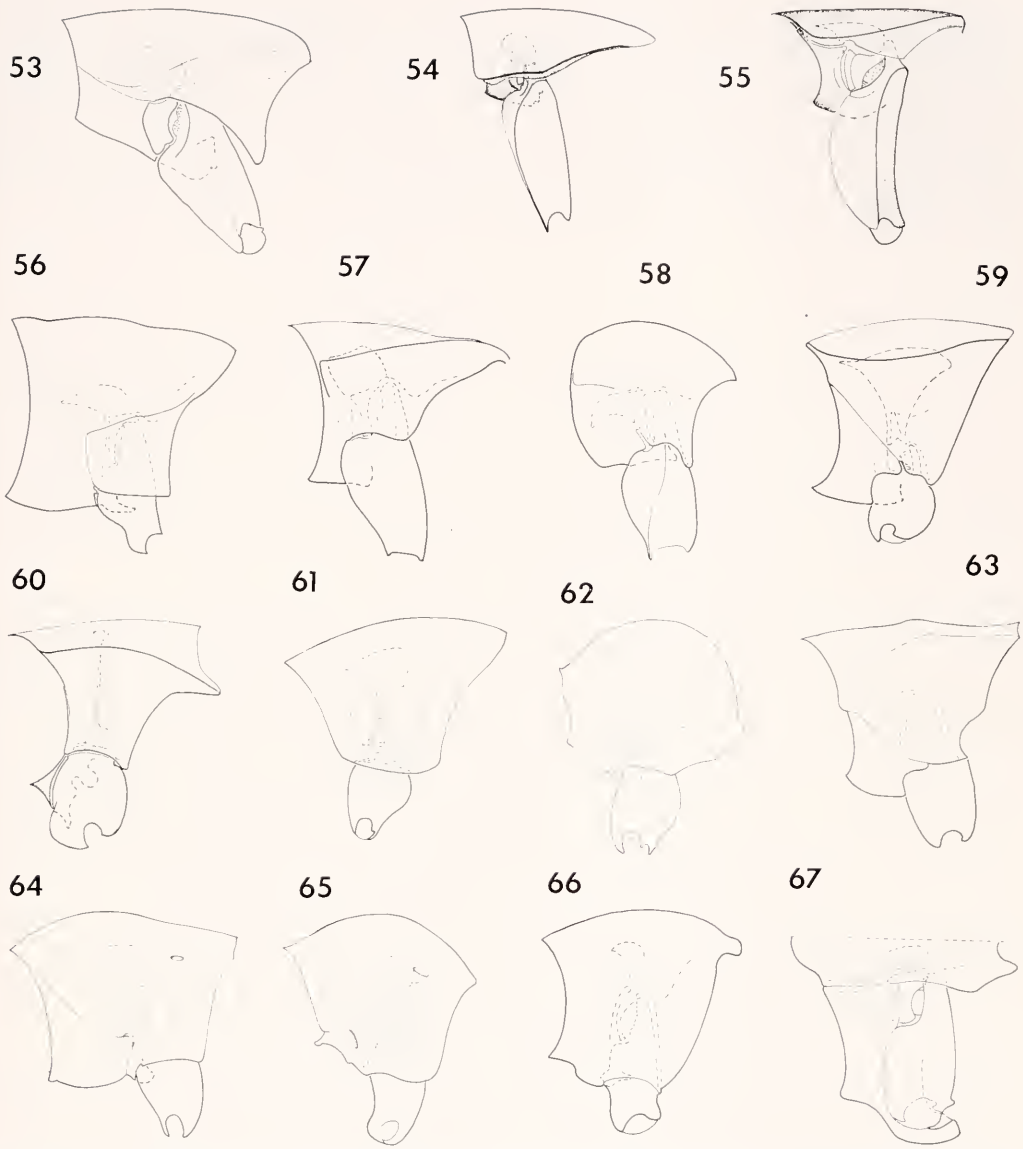
Pleuronotal joint, and quality of pleural motion, highly variable. Pleuron may be capable of rotation and a slight amount of flexation in the proteinines, omaliines examined as well as in *Siagonium*, *Trigonurus*, *Oxyporus*, and *Tachinus*. In *Osorius*, a large ventrally directed condyle on the notal fold articulates with a small concave region on the dorsal face of the coxa. Among the forms with deep coxal internalization, there are no condyles in *Piestus* and *Stenus*, but in *Oxytelus* and *Bledius* a small evagination on the pleuron, below the apophysis and anterior to the coxae, is inserted into a cavity in the notal cowling, while in *Leptochirus* a large notal condyle articulates with both the coxa and pleuron. In the high flexing forms, the margin of the curved invagination encloses a large flat pleural surface which is in contact with and moves against the flat surface of the notal cowling during flexation, e.g., *Philonthus*, *Lathrobium* (Figs. 132–133).

Coxal structure, enclosure and motility highly variable. In many generalized forms, only the strong dorsal pleurocoxal articulation is enclosed within the notum, and a portion of the coxae may be enclosed by the notal projection, e.g., *Proteinus*, *Omalium*, *Trigonurus*, *Tachinus* and *Oxyporus* (Figs. 44–46, 49, 52). In these forms the pleural articular region of the coxa is broad and generally more than .30 coxal length as in *Trigonurus* (Fig. 144). Dorsal development of the pleurocoxal cowling results in enclosure of the entire articular region in *Oxytelus* and *Bledius* (Figs. 57–58) or of enclosure below the articular region as in *Stenus* (Fig. 56). The articular region is about .60 total coxal length in both *Piestus*, where it is partially enclosed, and in *Leptochirus* (Figs. 48, 51, 145), where it is entirely enclosed. The very narrow articular region is reduced to less than .25 coxal length in high flexing forms such as *Philonthus* (Figs. 54, 146), where it is partially enclosed and in *Aleochara* and *Lathrobium*, where the articular region is almost entirely external. Coxal flexation is prevented by the shape and position of the notal projection in *Leptochirus*, *Piestus*, *Bledius*, by the contours of coxal cowling in *Stenus* and by a long coxal carina which is inserted into a groove in the cryptosternum in *Lispinus* and *Osorius*.

Pleurocoxal articulation usually well-developed, involving a conical projection on the coxa that is inserted into a depression on the pleuron.

Promesothoracic joint highly variable and not studied in detail. In generalized forms the notal projection rests on the mesepisternum and the pronotum rests on the mesonotum and elytra resulting in somewhat rigid (*Trigonurus*) to relatively loose connections (*Omaliinae*). In some of these forms there are small cavities in the mesosternum for reception of the procoxae. The very loose joint in some of the high flexing forms, e.g., Staphylininae, is similar to that of higher silphids, e.g., *Nicrophorus* (Fig. 41). A motile joint with structural integrity is found only in *Leptochirus*.

Mesothoracic spiracle surrounded by sclerotized margin that is usually produced ventrally and is triangular in outline. In the



Figures 53–67. Staphylinoidea. 53. *Lathrobium prahae*. 54. *Philonthus cyannipennis*. 55. *Aleocharara lata*. 56. *Stenus juno*. 57. *Oxytelus fuscipennis*. 58. *Bledius* sp. 59. *Scaphium castanipes*. 60. *Schaphisoma castanium*. 61. *Connophron flavicarse*. 62. *Clidicus* sp. 63. *Chevrolatia amoena*. 64. *Sonoma tulnae*. 65. *Tmesiphorus costailis*. 66. *Fustiger fuschi*. 67. *Micropeplus laticollis*.

piestines and in most omaliines examined, the slender spiracular sclerites reach but are not fused with a median intersegmental sclerite. However, in the omaliine genera *Phaleopterus* and *Trigonoderus*, the median sclerite is absent. The spiracular sclerite in *Proteinus* (Fig. 44), *Megarthrus* and *Tachinus* (Fig. 49) is large and articulates with and is partially enclosed by the notum; in the latter two genera there is also an

articulation with a small median sclerite. In *Pinophilus,* either the intersegmental membrane, the spiracular sclerites or both are fused to each other and to the notal projection and sternum to form a functionally closed coxal cavity that serves as a posterior limit to coxal flexation (Blackwelder, 1936, Fig. 238).

MICROPEPLIDAE
Figure 67

Head prognathous, cervical sclerites present. Notum with large flat lateral margins bearing large cavities on their ventral surfaces for reception of antennae. A very small notal projection extends for short distance anteriorly to overlap sternum. Notosternal joint membranous. Sternum: exosternum narrow and high, projection broad, extends beneath coxae and fits into shallow cavity on the mesosternum.

Pleuron motile attached to notum near rim. Endopleuron small, does not extend far above notosternal joint, with broad base and slightly expanded apex. Pleural rim-fold small, does not extend below pleurocoxal articulation.

Dorsal pleurocoxal articulation enclosed, articular region of coxa not constricted, .31 total length. Groove on inner surface of coxa, near apex, fits into groove on endosternum limiting coxal motion to rotation.

Promesothoracic joint may be rigid, posterior margin of notal projection fits into cavity on mesepisternum, while the sternal projection fits into a depression on mesosternum and the elytra and pronotum overlap broadly. Small mesothoracic spiracles attached to a slender creased sclerite.

DASYCERIDAE
Figure 38

Head prognathous, cervical sclerites present. Notum with slightly produced lateral margin that is lined with a row of elongate seta-bearing projections. Such projections along with those on the notal disc are most heavily encrusted with waxy detritus. Notosternal suture absent.

Pleuron fused to broad notal cowling. Endopleuron with slender base and flared apex. Articular region of coxa reduced, partially enclosed by broad notal cowling and projection; trochantin concealed by sternal cowling.

BRATHINIDAE
Figure 34

Head prognathous, constricted posteriorly into slender neck, cervical sclerites present.

Notum ovoid in cross section, with reduced lateral margins, projection triangular in outline reaches level of trochantinal apex. Notosternal joint rigid, inclined, notal fold present.

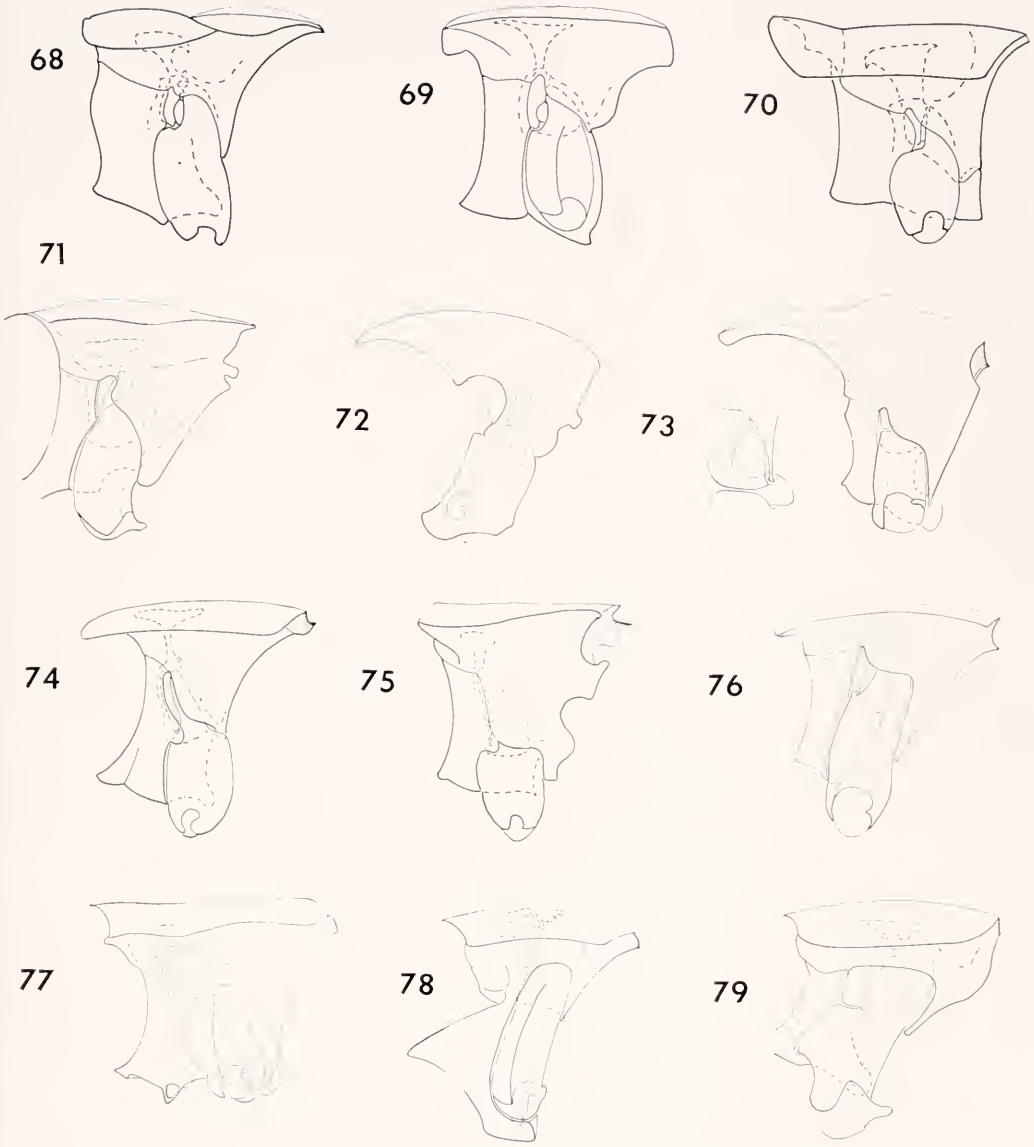
Sternum extends slightly below trochantin, projection small, acts as coxal separator. Pleuron motile, attached to notum near rim. Endopleuron with broad base and slightly expanded, apex. Trochantin broad, folded lengthwise. Internally a small pleural rim-fold is present but does not extend below the pleurocoxal articulation. Coxa capable of flexation. Articular region .26 total length, not compressed laterally, dorsal articulation of projection cavity type.

Loose promesothoracic joint, with small procoxal cavities on the mesosternum.

HYDRAENIDAE
Figures 68–70

Generalized configurations with partial trochantinocoxal enclosure and ventrally closed coxal cavities in *Hydraena,* but with dorsally closed coxal cavities in *Limnebius.*

Head prognathous, posterior aspect enclosed by prothorax, cervical sclerites present. Anterior face of notum bears a pair of cavities which enclose some of the eyes, the antennae are housed in a slight (*Limnebius*) or elongate (*Hydraena, Ochthebius*) posterior elements of these cavities. In *Hydraena,* the long maxillary palpi can be placed in narrow grooves extending from



Figures 68–79. Staphylinoidea, Hydrophiloidea, Histeroidea, Scarabaeoidea. 68. *Ochthebius* sp. 69. *Limnebius piceus*. 70. *Hydraena pennsylvanica*. 71. *Spercheus* sp. 72. *Georhyssus californicus*. 73. *Epimetopus costatus*. 74. *Enochrus pygmaeus*. 75. *Helophorous* sp. 76. *Sphaerites politus*. 77. *Syntelia mexicana*. 78. *Hister sulcatus*. 79. *Pleocoma* sp.

below the antennal cavities to the posterior margin of the notum.

Notal projection present, not connected with sternum only in *Ochthebius* (Fig. 68). Rigid notosternal joint, horizontal to slightly inclined, suture difficult to see in *Limnebius*. Cryptosternum variable, solidly fused to notum producing dorsal closure of coxal cavities in *Limnebius* (Fig. 69). In *Hydraena* (Fig. 70) the sternal projection

is expanded behind the coxae; its lateral edges fit into slight cavities in the notal projection producing ventral closure of the coxal cavities. The sternal projection also forms a vertical coxal separator; its dorsal surface is expanded and flattened and rests against the mesosternum.

Pleuron movable, attached to notum near rim. Stalk of endopleuron squat (*Hydraena*) or slender (*Limnebius, Ochthebius*), all with flared apex. Trochantin folded lengthwise with large rim-fold. Most of coxal articular region and trochantin enclosed by sternal and notal cowlings in *Hydraena* (Fig. 70), less coxal enclosure in the other genera.

PTILIIDAE AND LIMULODIDAE
Figures 34, 35

Specialized configurations with dorsally closed coxal cavities or with cavities nearly closed. Pleuron rigid, trochantin and slender coxal articular region enclosed.

Head prognathous, posterior aspect inserted into prothorax, deeply so in *Limulodes*. Cervical sclerites absent. Lateral margin of notum greatly expanded in *Limulodes*, less so in *Acratrichis*, only slightly expanded in *Nossidium* and *Nannosella*. The notal projection of *Acratrichis* fused broadly with sternum at level of trochantinal apex, forming dorsally closed coxal cavities, suture absent (Fig. 35). In *Nossidium* the notum and sternum come close together but do not touch, a notal short projection that arches over the posterior coxal face is also present (Fig. 34).

Notosternal joint solid, suture absent except in *Acratrichis*. Complete enclosure of coxal articular region and trochantin has resulted from the fusion, after overlap, of the notal and sternal cowlings. Only a small area of overlap is present in *Nossidium*.

Exosternum slender, cryptosternum broad, small median projection forms coxal separator. However, in *Limulodes* a long, broad projection extends beneath the pro- and mesocoxae and reaches the metasternum. A broad carina on the mesosternum fits into a medial groove on the prosternal projection.

Pleuron immovable, joined broadly to notal fold above coxa (Fig. 35). Endopleuron with long slender stalk and flared apex which extends to dorsal surface of the notum in *Limulodes* and *Acratrichis*. Trochantin slender, enclosed.

Coxae globose or cylindrical, articular region short, narrow and completely enclosed. Notal projection (*Nossidium*) and a coxosternal articulation (*Limulodes*) prevent posterior coxal flexation.

LEPTINIDAE
Figure 37

Generalized, somewhat flattened high volume configurations.

Head prognathous, narrowed posteriorly, cervical sclerites absent. Notum, lateral margins expanded. Notal projection small, reaches middle of trochantin, except in *Platypsyllus* where it is absent. Notosternal joint inclined, solid, suture present.

Sternal projection reaches coxal apex in Leptinus, expanded beneath coxae in *Leptinillus* and in *Platypsyllus* where it extends far beyond the coxae to rest on the mesosternum.

Pleuron with long connection with notal fold above coxa may be capable of movement. Endopleuron with slender stalked base and flared apex that extends up to and touches the dorsal wall of the notum. Coxae globose, articular region somewhat compressed, .38 total length.

Promesothoracic connection unspecialized except in *Platypsyllus* where the notum broadly overlaps the elytra. The long sternal projection rests on the mesosternum and the intersegmental membrane is unusually short, thick and tough.

SCAPHIDIIDAE
Figures 59, 60

High notal volume variably specialized configurations. Pleuron rigid, and fused

dorsally to notum in *Scaphisoma,* but not in other genera. Coxal articular region narrowed may be short and enclosed along with region slightly below it. External portion of coxa about as long as wide.

Head hypognathous in *Scaphisoma,* nearly prognathous in *Scaphium*, intermediate in *Scaphidium*, posterior aspect completely enclosed by prothorax, cervical sclerites present. Notum with neither expanded lateral margin nor posterior concavity for reception of part of the proleg; projection absent. Notosternal suture rigid, sharply inclined.

Sternum relatively broad in *Scaphium* (Fig. 59) less so in *Scaphidium*. The sternum is compressed dorsally in *Scaphisoma* (Fig. 60) into a narrow peninsula but is expanded at the level of the trochantin. In front of coxa it is molded into a small flat triangular vertical region on which the head rests. Sternal projection forms vertical coxal separator, and in *Scaphisoma* it is fused with the notal flange at the level of the coxal constriction, forming dorsally closed coxal cavities.

Pleuron rigid, with long notal joint above coxa. Endopleuron large with a broad base in *Scaphium* and *Scaphidium*, apex in contact with wall of notum. However, the slender stalk of *Scaphisoma* is only slightly expanded before fusing with the notum. Trochantin and pleuron solidly fused to notum and reduced to a medially projecting shelf in *Scaphisoma*; not reduced in other genera.

Coxae capable only of rotation, constricted and enclosed below the narrow articular region, latter reduced to .16 total coxal length in *Scaphisoma*. A coxal carina in *Scaphium* and *Scaphidium* is inserted into a groove on the rim of the cryptosternum.

Trochantin, articular region of coxae and the constricted portion below it are completely enclosed in *Scaphisoma* and *Scaphidium,* while in *Scaphium* the rims of the cowlings do not overlap, but are quite close together at the level of the trochantinal apex.

Promesothoracic joint is rigid. In *Scaphidium* a condyle on the mesepisternum fits into a concavity on the posterior notal flange, while in *Scaphium* an elongate ridge on the flange is inserted into a furrow on the mesepisternum. The notal flange is *Scaphisoma* bears both a condyle, which is placed into a concavity on the mesepisternum, and also a long furrow which receives the sharp edge of the episternum. The anterior face of the mesosternum bears two large concavities for housing the procoxae.

SCYDMAENIDAE

Figures 61–63

High notal volume specialized configurations leading to forms with very reduced horizontal sterna, e.g., *Connophron* (Fig. 61). Coxa enclosed below trochantin. Pleuron rigid.

Head prognathous, not constricted posteriorly in *Cephennium*. In the other genera examined the head is hypognathous and constricted posteriorly to form a large globose articular region that is only partially enclosed within the prothorax. Cervical sclerites present, small.

Notum highly developed in some but without expanded lateral margins or posterior medial curvature, projection absent. Notosternal suture rigid when present, inclined in *Chevrolatia,* horizontal in *Cephennium*.

Sternum variable. In *Chevrolatia* (Fig. 63), *Lophioderus, Ascydmus, Veraphis* and *Mastigus,* the exosternum is distinct with a lateral connection to the notum, while in *Leptoscydmus* and *Clidicus* (Fig. 62) an exosternum is present, but the notosternal suture is absent. The exosternum of *Cephennium* is reduced to a small triangular region below the notosternal suture. In *Scydmaenus, Eumicrus* and *Connophron* (Fig. 61) the notum is expanded ventrally so that its lateral margin is actually ventrad

of the approximately horizontal sternum. In *Connophron*, at least, there is no differentiation of the sternum into exo- and cryptosternum. Sternal projection absent, except in *Cephennium* where it is vertical and reaches the coxal apex. Posterior sternal and notal flanges fused at level of trochantin in *Connophron* forming dorsally closed coxal cavities, projections widely separate in *Clidicus*, less so in *Cephennium*.

Pleuron apparently immovable, attached broadly onto notum. Endopleuron with slender stalk and expanded apex in *Connophron* (Fig. 61) and *Cephennium;* not so differentiated in *Clidicus* (Fig. 62). Trochantin completely enclosed, long and broad in *Clidicus*, short and narrow in *Connophron* and *Cephennium*.

Coxae capable only of rotation, constricted and enclosed for short distance below trochantinal apex. Articular region of *Connophron* not parallel with long axis; coxal rotation causes anteroposterior movement of the coxal apex. Articular region long, broad in *Chevrolatia*, *Clidicus*, shorter and compressed in *Connophron* and *Cephennium*.

Trochantin completely enclosed by dorsal development of notal cowling in *Clidicus* and by overlap of notal and sternal cowlings in *Connophron*; probably by a combination of the two methods in *Chevrolatia*.

In most scydmaenids the pronotum rests broadly on the elytra and mesothorax, the prosternum overlaps the anterior rim of the mesosternum; the latter bears a pair of large concavities, usually separated by a carina, for the reception of the procoxae. In rest position, the prothorax may not be capable of much movement. The promesothoracic joint of the Clidicini seems less rigid, and lacks large mesosternal concavities.

PSELAPHIDAE
Figures 64–66

High notal volume specialized configurations with reduced sterna and with the coxae enclosed far below the trochantin.

Head prognathous in *Sonoma, Euplectus, Fustiger* inclined somewhat ventrally in *Tmesiphorus*, constructed posteriorly into a large globose condyle that is partially inserted into the prothorax. Cervical sclerites absent.

Notum developed far ventrally, with a long cowling; projection absent, without expanded lateral margins and posterior medial curvatures.

Notosternal suture faint and inclined in *Sonoma* where it extends along a shallow groove, absent in *Euplectus*, *Tmesiphorus*, and *Fustiger*. Sternum variable, exosternum relatively long in *Euplectus* and *Sonoma* (Fig. 64) smaller in *Tmesiphorus* and *Fustiger* (Figs. 65, 66).

Pleuron rigid or capable of slight movement, attached to notum far above notal rim but only slightly above the coxa. Endopleuron with broad base and moderately expanded apex. Trochantin long, enclosed. Coxae probably capable only of rotation, long, enclosed by notum far below trochantin. Articular region long, not constricted.

The pronotum rests broadly and snugly on the mesothorax; the procoxae are housed by an undivided cavity on the mesosternum.

HYDROPHILOIDEA
Figures 71–75

(Except *Georyssus*). Specialized configurations with dorsally closed coxal cavities and in *Epimetopus* ventral closure as well. Coxal articular region and trochantin always partially enclosed, completely so in *Helophorus, Hydrochus* and *Georyssus*. Pronotum-elytra interlocking device always present, while a strong ventral interlocking mechanism is present in some Hydrophilinae.

Broad, prognathous head deeply inserted into prothorax. Cervical sclerites present.

Lateral margin of notum varies from reduced in *Epimetopus* to large and flattened in *Enochrus*. Posterior wall and

notal carina present, former bears striate crenulations in *Spercheus*.

The notal projection of *Epimetopus* (Fig. 73) is long and gradually narrowed below the dorsal closure, its apex rests on the sternal projection; a large foramen is enclosed between the notal projection and the cryptosternum. In *Helobata* and *Hydrochus*, however, the dorsal closure is very broad and the short blunt projection reaches the sternal projection but no foramen is enclosed. In the other genera examined a short, blunt projection extends slightly below the dorsal closure, e.g., *Enochrus* (Fig. 74).

Notosternal joint short, horizontal or nearly so, rigid to tightly membranous with internal carina.

Exosternum reduced, extends little in front of coxae in *Chaetarthria* and *Berosus*, slender in other genera, does not reach coxal apex; with low carina along ventral midline in *Enochrus, Berosus* and *Sphaeridium* while in *Tropisternus* and *Hydrophilus* the exosternum is broadly produced ventrally and bears on its posterior surface a large fossa. Dorsal surface of projection expanded and flattened forming a posterior sternal flange, in *Sphaeridium* it is highly concave.

Pleuron motile, except *Sphaeridium*, attached to notum near rim. Endopleuron with slender stalk and expanded apex, comes close to dorsal wall of notum, except in *Spercheus* (Fig. 71) where the base is squat. Trochantin usually slender, with narrow rim fold. What may be a pleurotrochantinal suture is present in *Spercheus*. In *Sphaeridium*, the pleuron is broadly fused to the notal rim and the endopleuron comes close to the dorsal wall of the notum. The trochantin is thin, poorly sclerotized and moves, along with the pericoxal membrane, as the coxa rotates.

Coxa capable of rotation only. Articular region long and narrow, usually more than .3 total length except in *Epimetopus* where it is short (.2 total length) and broad.

Coxal enclosure variable, occurs only through development of notal and sternal cowlings below notosternal joint. Little enclosure in *Chaetarthria*, coxal articular region and most of trochantin enclosed in majority of genera examined, e.g., *Epimetopus, Spercheus, Enochrus*. In *Sphaeridium* the cowlings come close together while in *Helophorus* (Fig. 75) they overlap to the level of the trochantinal apex and in *Hydrochus* cowling overlap extends below the trochantinal apex.

Promesothoracic joint relatively complex, not studied in detail. Notal carinae inserted into cavities in the elytra. Dorsal margin of notum usually overlaps dorsal margin of elytra; they meet edge-on in *Epimetopus, Hydrochus* and in *Spercheus*, where finely striate notal crenulations interdigitate against the finely striate dorsal rims of the scutellum and elytra. Dorsal surface of sternal projection generally in contact with mesosternum. In some hydrophilines a large mesosternal keel is inserted into a fossa on the posterior face of a sternal projection forming an interlocking device which could prevent lateral movements of the prothorax. In *Sphaeridium* a blunt condyle on the mesosternum is received by a cavity in the sternal projection.

Georyssus

The prothorax of *Georyssus* (Fig. 72) is modified to form part of a highly developed head-prothorax-mesothorax compacting mechanism. The head in rest position is opisthognathous and housed in a large, complex cavity formed posteriorly by the nearly continuous vertical faces of the pro- and mesosternum and laterally by the large, flattened medial coxal surfaces. The coxae are produced, below the trochanteral insertions, into large medially curving plates that partially cover the mouthparts and labrum. The antenna is housed in a large cavity formed from the notum and the small lateral regions of the sternum. The notosternal suture and probably a zone of cowling overlap occur in

this cavity. The flattened medial surface of the femora can close the entrance to the antennal cavity.

Coxal articular region and trochantin enclosed. Endopleuron with broad base and horizontal apex. Coxal cavities closed dorsally. Posterior wall and small notal carina present.

HISTEROIDEA

Figures 76–78, 137–139

Specialized rigid body, high notal volume configurations with extreme dorsal enclosure of the trochantin and coxa and with a complex compacting mechanism, e.g., *Hister* (Fig. 78) *OR* with partial coxal enclosure but without compacting and interlocking mechanisms, e.g., *Sphaerites*, *Syntelia* (Figs. 76, 77). There is great variation in the pleurocoxal mechanism leading up to a scarabaeoid type in *Hister*, compare Figures 139, 140.

Head is hypognathous in *Sphaerites*, *Hister* and in *Saprinus* where it is, in rest position, deeply enclosed within the pronotum partially to wholly concealing the eyes; head prognathous in *Syntelia* and *Hololepta*. A small (*Saprinus*) or large (*Hister*) anterior expansion of the sternum conceals the mouth parts up to near the mandibular apices, while laterally a slit cavity device houses the antennae. Cervical sclerites present.

Posterior notal wall present, its ventral rim only slightly expanded. Notal projection long in *Sphaerites* (Fig. 76) and *Saprinus*, short in *Hister* (Fig. 78) and *Hololepta*. Notal projection is attached to the sternal projection forming ventrally closed cavities only in *Syntelia* (Fig. 77).

Notosternal joint solid, suture inclined ventrad from coxa in *Hololepta* and *Saprinus*, only slightly so in *Hister* and *Sphaerites*. Sternal and notal folds distinct in *Sphaerites*, reduced in other genera.

In *Saprinus* and *Hister*, the exosternum is produced medially into a large horizontal flange, laterally it is narrowed and bears a groove and a cavity that house the basal antennal segments and the antennal club respectively. *Sphaerites* and *Syntelia* lack both an expanded sternum and an antennal housing mechanism, a slightly expanded sternum is present in *Hololepta*. Cryptosternum narrow in *Sphaerites*, broad, reaching level of notal projection, in *Saprinus*, *Hister* and *Hololepta*. Sternal projection slender, acts as coxal separator and does not reach coxal apex in *Syntelia* and *Sphaerites*, while in the other genera examined it is broad and extends beneath the coxa.

Pleuron motile, attached to notum at or near level of dorsal wall. Endopleuron distinctly shifted anteroventrally in *Hister* (Fig. 139), less so in *Saprinus* (Fig. 138), relatively unmodified in *Sphaerites* (Fig. 137) with a triangular ventral carinae in *Hister* and *Saprinus*. Trochantin broad, partially exposed in *Sphaerites* where it is folded lengthwise nearly 90° and has a large rim-fold; boundary between pleuron and trochantin obscure, it may form the ventral margin of pleurocoxal articulation cavity. In *Saprinus* there is a distinct zone of fusion between the trochantin and exopleuron below the pleurocoxal articulation, fusion zone compressed in *Hister*.

Coxae very long, capable only of rotation. Articular region broad, about .3 total length, enclosed except in *Sphaerites*. Coxa articulates with sternal projection via a groove-ridge device in *Hister* and *Hololepta*.

Sphaerites, *Saprinus* and *Hister* represent successive steps in the development of a scarabaeoid type pleurocoxal mechanism. In *Sphaerites* the pleurocoxal cowling is developed far dorsally but is not fused to the lateral or dorsal notal walls and does not bear a condyle; the pleurocoxal articulation is of the projection-cavity type and is similar to that of other staphyliniforms, as is the structure of the trochantin and endopleuron (Fig. 137). In *Saprinus* the cowling bears a strut that is fused to the lateral notal wall and comes close to, but is not fused with, the dorsal notal wall. A pleural projection articulates with the con-

cave dorsal face of the coxa, while the endopleuron extends ventrally as a slender peninsula (Fig. 138). In *Hister* the cowling is fused not only to the lateral notal wall, via a strut, but also to the dorsal wall. It bears a large condyle that is inserted into a cavity formed from the pleural projection and from the coxa above the pleural articulation. The endopleuron is developed and expanded far ventrally (Fig. 139).

Promesothoracic joint relatively loose in *Sphaerites*; the perpendicular posterior face of notum rests against the elytra blocking dorsal rotation. The mesosternum is without cavities for reception of the prosternal projection and procoxae. *Syntelia* is a somewhat pedunculate form; the prothorax is capable of rotation above the plane of the elytra.

Saprinus and *Hister* are rigid-body compacted forms. Dorsally, the perpendicular faces of the notum and elytra lie against one another, and a small notal carina is inserted into a groove on the elytra or mesepisternum. The mesepisternum is developed far in front of the elytra forming a broad shelf on which the pronotum rests. The mesepisternum also curves medially and meets the notal projection to form a cavity that can house the profemur in rest position. The mesosternum bears a pair of divided cavities that receive the procoxae and in *Hister* it also bears a cavity that receives the prosternal projection. In *Saprinus* the prosternal projection overlaps the mesosternum for a short distance; ventral motion of the prothorax is blocked by a vertical ridge on the projection.

SCARABAEOIDEA

Figures 79–84, 140, 148

Moderate to high notal volume forms with a uniform, specialized, pleurocoxal mechanism with extensive ventral shift of the endopleuron. Coxal cavities closed ventrally, except *Pleocoma*.

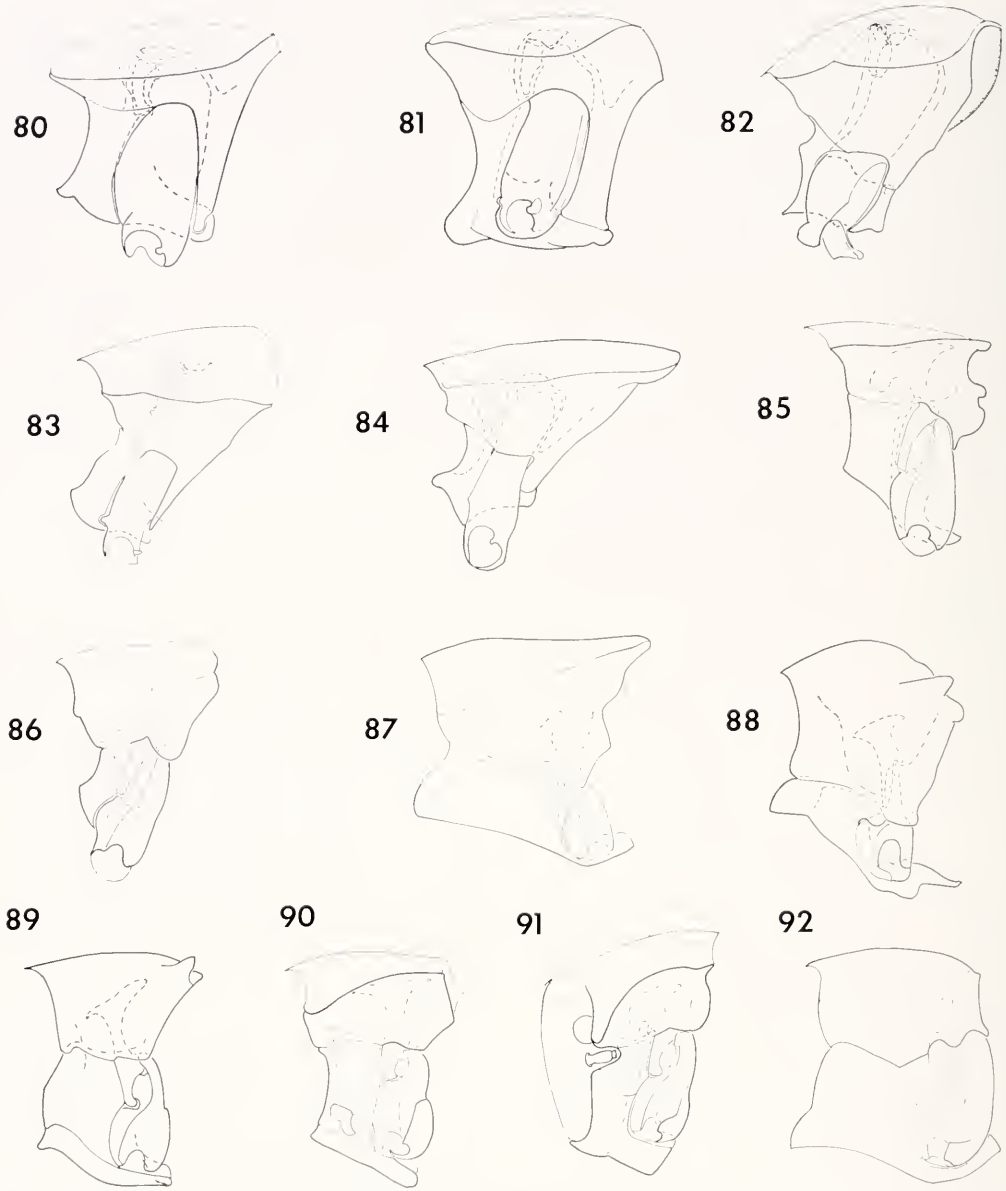
Notal height and enclosed volume varies greatly in the forms examined. The very low notum of *Pleocoma* (Fig. 79) encloses about half the exopleuron and trochantin; the sternum is high. In many forms the notum reaches the level of the trochantinal apex, e.g., *Popilius, Cerucheus* (Figs. 80, 81), while in a few it is developed far below the trochantinal apex, e.g., *Phyllophaga, Copris* (Figs. 83, 82) and the sternum is reduced. Size and shape of notal projection variable, its apex is loosely or tightly enclosed by grooves or cavities on the sternal projection forming ventrally closed coxal cavities, except in *Pleocoma* (see Ritcher, 1969, Figs. 2–10). Posterior wall sometimes present but never bears interlocking mechanisms.

Notosternal joint solid, inclination of suture varies from straight and horizontal to slightly inclined and curved.

Exosternum narrow, normally extends to just above coxal apex, comes close to being horizontal in some high notal volume forms, e.g., *Copris*. Sternal projection compound, very large evagination of sternellum forms a large flange, and laterally bears grooves or a pit that receives the notal projections.

Pleuron motile, attached to notum at level of dorsal wall, rotates, along with the coxa, about notal condyle (Fig. 140). Endopleuron vertical, shifted anteriorly so that most of it is anterior to rather than above the exopleuron. A distinct pleural invagination is present dorsally but is obscure anteriorly. The exo- and endopleura are developed ventrally resulting in reduction of the trochantin. In *Lichnanthe* (Fig. 134) the trochantin and its internal rim fold are somewhat reduced, comparable to the condition in *Hister* (Fig. 139), but in most other Scarabaeoidea, e.g., *Phyllophaga* (Figs. 83, 140), the endopleuron reaches quite close to the trochantinal apex so that the rim fold is either greatly reduced and difficult to see or is absent. Ventral surface of endopleuron usually carinate.

Pleurocoxal articulation and manner in which both articulate with and rotate about the notal condyle without appreciable vari-



Figures 80–92. Scarabaeoidea, Elateriformia. 80. *Ceruchus piceus*. 81. *Popilius disjunctus*. 82. *Corpis fricator*. 83. *Phyllophaga* sp. 84. *Euphoria lambalis*. 85. *Dascillus davidsoni*. 86. *Sandalus niger*. 87. *Brachypsectra fulva*. 88. *Cerophytum elateroides*. 89. *Eurypogon niger*. 90. *Artematopus puncticollis*. 91. *Byrrhus americanus*. 92. *Heterocerus pallidus*.

ation in the scarabaeoids examined. A bar-like pleural evagination with a concave surface articulates with the coxa, and receives a portion of the notal condyle. The coxa extends above the pleural articulation and bears a concave surface that articulates with the notal condyle (Fig. 148).

Coxa always with strong notal articu-

lation as described above, capable of rotation only, articular region broad (varies from .25–.4 total length), wholly enclosed, except in *Pleocoma*. A very broad attachment surface for posterior rotator muscles always present, coxal foramen large, ovoid, usually extends far below articular region (Fig. 148). In many forms examined, a coxal carina is inserted into a groove in the cryptosternum, e.g., *Phyllophaga, Popilius*, while in *Copris* the groove is on the coxa and the ridge on the cryptosternum. Otherwise, a coxo-sternal articulation may be absent, e.g., *Ceruchus*.

Series **ELATERIFORMIA**

A large assemblage of limited diversity. Putative stem form with membranous notosternal joint, generalized pleurocoxal mechanism, low notal volume, and a suite of promesothoracic interlocking devices including striate crenulations which serve as a defense mechanism or as a semipermanent rigid joint (e.g., Ptilodactylidae, and some dascilloids, psephenids, dryopids). Major elements of variation: (1) Malacodermization, involving variable reduction of interlocking devices as well as exposure of head and trochantin and possible extensive exposure of intersegmental membrane, plus variable modification of the pleurocoxal mechanism to permit extensive flexation; Psephenidae (*Eubrianax, Pheneps*); Dryopidae (*Lara, Potamophilus*); Dascillidae (*Anorus*, karumines); Cantharoidea, Cebrionidae (*Scaptolenus*), Artematopidae, Rhipiceridae (*Sandalus*), Ptilodactylidae (Some exotic anchytarsines). (Figs. 86, 93, 97, 110, 113–116.) (2) Development of a quasi-permanent rigid-body configuration involving reduction of the assumed primitive interlocking structures, e.g., Artematopoidea, Byrrhidae, Elmidae, Buprestoidea. (Figs. 90, 91, 98, 106, 107, 118, 119.) (3) Transformation of interlocking devices into the articulations of a startle defense mechanism has occurred in the elaterids and possibly in some members of related families. (4) Compaction of pro- and mesolegs in thoracic cavities so that they lie flush against surrounding surfaces e.g., Chelonariidae, Psephenidae (*Dicranopselaphus*), Byrrhidae, Throscidae, Eucnemidae, Buprestidae (*Tachys*). (Figs. 91, 105, 166.) Enclosure of antennae and mouthparts also common.

Pleurocoxal mechanism generalized in most taxa, with the motile trochantin exposed or only slightly enclosed e.g., *Dascillus, Eurypogon, Dicranopselaphus, Stenocolus* (Figs. 85, 89, 94, 100). Deep enclosure of an elongate coxal articular region found only in *Ptilodactyla* and related genera and in *Cerophytum*. Enclosure less extensive in *Brachypsectra* (Figs. 87, 88, 104). Enclosure of a reduced coxa and trochantin is associated with loss of pleural motility in most elateroids; pleural fusion and coxal reduction without enclosure characterizes the buprestoids (Figs. 106–109, 118–119). Coxal cavities never closed.

The promesothoracic joint of many elateriforms consists of a complex set of interlocking mechanisms. Three major zones of contact bear specialized attachment structures: (1) Posterior dorsal face of the notum and the anterior region of the mesonotum plus the elytra; (2) Posterolateral region of the notum and the mesepisternum, and sometimes the mesepimeron as well; (3) The prosternal projection against a cavity or groove on the mesosternum. In addition, the coxae are often housed in paired cavities formed from the inflected anterior faces of the mesosternum and sometimes the mesepisternum (Figs. 159–161).

The entire posterior dorsal rim of the notum bears hemicylindrical transversely striate crenulations in many groups (Ptilodactylidae, all; Chelonariidae; Psephenidae, e.g., *Sclerocyphon*; Dryopidae only *Pelonomus*; some species of *Dascillus* and *Rhipicera marginata* (Fig. 159, Crn)). These

crenulations may fit against a complementary set on the elytra and scutellum. In other elateriforms, notal striations may be present but without crenulations (Callirhipidae), or with at most a single pair (Elateriodea). In most groups, even those without crenulations or striations, the notal rim is slightly expanded to form triangular paramedial projections which fit against the elytra-scutellum (Fig. 160). In *Brachypsectra* only these projections bear faint striations.

In many forms the ventral margin of the posterior notal face bears a pair of globose condyles which fit into concavities on the mesonotum (Figs. 159–160 MCnd). The posterior face bears a pair of ridges which are placed in cavities on the anterior face of the elytra (Figs. 159–160 R). The lateral region of these notal carinae is sometimes expanded into a lateral condyle. Laterally the notal projection may be modified to increase the degree of intersegmental overlap and can also bear interlocking devices. A flattened lobelike expansion which extends far behind the posterior wall may rest against concavities on the mesopleuron or elytra (Figs. 94, 100–105, 161). A condyle, groove or both at the base of this notal lobe interlocks with complementary structures on the mesepisternum (Fig. 159 NPj, LCnd). The sternal projection is often broad and housed in mesosternal cavities. Variation in attachment devices of rigid-body forms, which may not be mechanical, will be treated elsewhere, as will evidence supporting the tentative hypotheses for their having evolved from ancestors with interlocking mechanisms.

ARTEMATOPOIDEA

ARTEMATOPIDAE

Figures 89–90

Rigid-body forms without an interlocking system involving crenulations or striations on the posterior notal face; and with a generalized pleurocoxal mechanism.

BRACHYPSECTRIDAE

Figure 87

Posterior notal face with striations only on paramedial projections. Coxa and trochantin partially enclosed by cowlings. Sternal projection narrow, apparently capable of movement in a long, deep, mesosternal fossa similar to that of elateroids.

CEROPHYTIDAE

Figure 89

Quasi-rigid body forms of questionable systematic position, included here as a preliminary hypothesis. Posterior notal wall reduced, and with a unique and non-elateroid pleurocoxal mechanism. Coxal articular region long and completely enclosed along with the trochantin by cowlings. Endopleuron relatively small. The mode of coxal enclosure and geometry of pleurocoxal mechanism resemble that of *Ptilodactyla* and *Brachypsectra.*

DASCILLIODEA

Figures 85–86

Generalized, pleurocoxal mechanism-forms show much variation in degree of reduction of elateriformlike interlocking devices and in structural integrity. Striate crenulations present only in some species of *Dascillus* (Dominican Republic, India) and in *Rhipicera marginata.* Sternal projection lies far above coal apex in *Anorus* and *Karumia,* in the latter the posterior notal face is greatly reduced and lacks attachment devices. This malacodermization sequence is associated with specialized life cycles, including larviform females, parasitism and possibly terimitophily.

BYRRHOIDEA

BYRRHIDAE

Figure 91

Generalized pleurocoxal mechanism forms with a rigid promesothoracic attachment but without interlocking devices on pos-

terior notal face. Head enclosed to mouthparts. Antenna concealed between the legs and prothorax, pro- and mesothoracic appendages may lie flush in deep cavities as in Figure 164.

DRYOPOIDEA

PTILODACTYLIDAE
Figures 100, 102–105, 159–161

(Except Ptilodactylinae) Generalized configurations with the elateriform promesothoracic joint well developed. Complex variation present in the head-prothoracic joint and in relative heights of notum, sternum and trochantin.

Ptilodactylinae. As above, but with the elongate coxal articular region completely enclosed by overlap of cowlings and by dorsal migration of the notopleural articulation (Figs. 104, 159–161).

CHELONARIIDAE
Figures 105, 164

Generalized pleurocoxal mechanism and elateriform type promesothoracic joint but with a very highly developed compaction system.

Anterior contours of head lie flush with notum and sternum, mouthparts concealed. Compacted pro- and mesolegs lie together in continuous pro- and mesothoracic depressions and are flush with surrounding surfaces (Fig. 165).

CALLIPHIPIDAE
Figure 101

Generalized configurations with a well-developed elateriform interlocking system quite similar to that of Ptilodactylidae, but with lateral crenulations weakly developed or absent. Sternum does not extend to coxal apex and does not enclose mouthparts.

PSEPHENIDAE
Figures 93–95

Generalized configurations with a somewhat (*Eubrianax, Sclerocyphon*) to very reduced elateriform interlocking system (*Psephenus, Pheneps*) where crenulations are absent and the posterior notal face is simple. Had usually hypognathous and deeply enclosed except in *Psephenus; Mataeopsephus* and *Pheneps* when it is nearly prognathous and the mouthparts are exposed.

HETEROCERIDAE
Figure 92

Pleurocoxal mechanism generalized. Prognathous head deeply enclosed, sternal flange broad. Promesothoracic joint loose, motile. Elements of interlocking system lacking, notum does not extend far beyond coxa.

LIMNICHIDAE
Figure 96

Rigid body forms without an interlocking system and with a generalized pleurocoxal mechanism. Head hypognathous, enclosed to eyes, mouthparts concealed (except Thaumastodinae). Antenna concealed between body wall and variably compacted pro- and mesolegs.

DRYOPIDAE
Figure 99

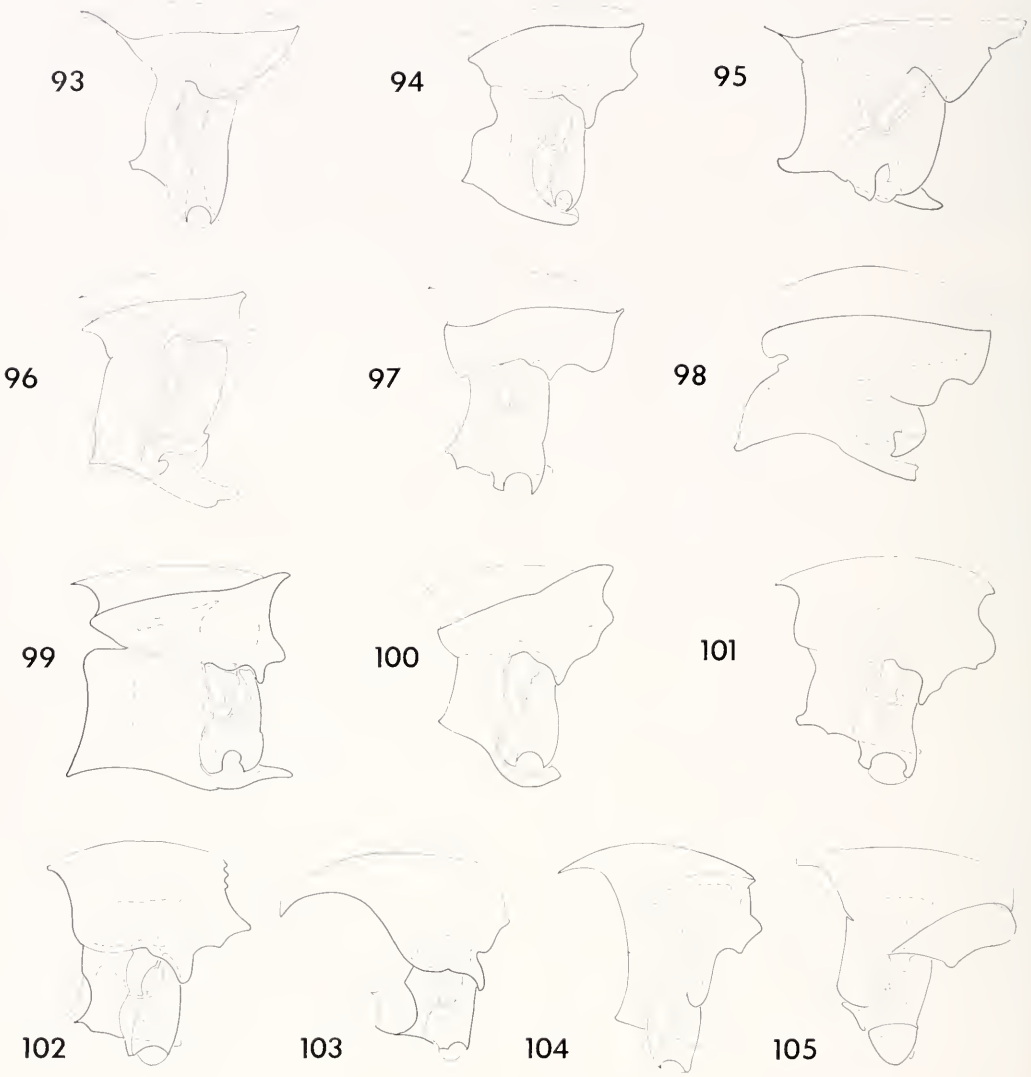
Rigid body forms with a generalized pleurocoxal mechanism. Hypognathous head enclosed to eyes; mouthparts, antennae concealed by sternum. Crenulations and associated elateriform interlocking structures present only in *Pelonomus*.

ELMIDAE
Figures 97, 98

Moderately variable configurations with the Larinae, Potomophilinae differing sharply from the Elminae.

In *Lara* (Fig. 97) the head is not deeply enclosed, the mouthparts and coxae extend below the narrow sternum, the trochantin is exposed and the promesothoracic joint is loose.

In *Stenelmis* (Fig. 98) the head, mouth-



Figures 93–105. Elateriformia. 93. *Eubrianx edwardsi*. 94. *Dicranopselaphus* sp. 95. *Psephenus* sp. 96. *Lutrochus geniculatus*. 97. *Lara amphipennis*. 98. *Stenelmis crenata*. 99. *Pelonomus obscurus*. 100. *Stenocolus scutellaris*. 101. *Zenoa picea*. 102. *Anchycteis velutina*. 103. *Araeopidius monachus*. 104. *Ptilodactyla serricollis*. 105. *Chelonarium lecontei*.

parts and coxal apices are enclosed by the broad sternum, the coxal articular region is reduced and enclosed by variable development to overlap of sternal and notal cowlings. Promesothoracic joint rigid, interlocking structures reduced. In some elmines e.g., *Cleptelmis* and *Heterlimnis* the mesepisternum is developed into a cowling which encloses much of the procoxa; the prosternal cowling encloses the trochantin.

ELATEROIDEA

Specialized, high notal-volume configurations with reduced and enclosed coxal articular regions. Pleuron rigid, may be fused to dorsal wall of notum; trochantin (sometimes extremely reduced) forms merely a part of the coxal articulation along with the notal rim-fold. Interlocking devices almost always present in rigid-body forms but these structures are modified into a "jumping" mechanism, in the Elateridae and probably some eucnemids. Notal crenulations usually absent or only a few occur; striations common.

CEBRIONIDAE
Figure 110

A reduction sequence complicated by sexual dimorphism. The prothorax of some, e.g., *Aplastus*, *Euthysanius*, differs little in structure from that of other elateriods. In others, *Cebrio*, *Scaptolenus*, the length of the sternum and the height of the notum are reduced while notal and sternal cowlings are also reduced to varying degrees exposing the coxal-articular region.

THROSCIDAE
Figure 106

Rigid-body compacted forms. Head deeply enclosed; mouthparts concealed; antennae enclosed in grooves. Pro- and mesolegs concealed in thoracic cavities and lie flush with surrounding surfaces. In the Balginae, the rims of elytra and pronotum are curved ventrally as in elaterids, these structures are coplanar in other subfamilies.

EUCNEMIDAE
Figure 107

Elateroidea with variation in antennal enclosure, compaction. Also variation in the promesothoracic joint.

In the Melasinae the legs are not compacted, the antennae not concealed in grooves, and in some the promesothoracic joint appears motile and is quite elaterid-like, e.g., *Anelastes*. While in the gastraulacines and eucnemines, the pro- and mesolegs are compacted in cavities, the antennae concealed in pronotal grooves.

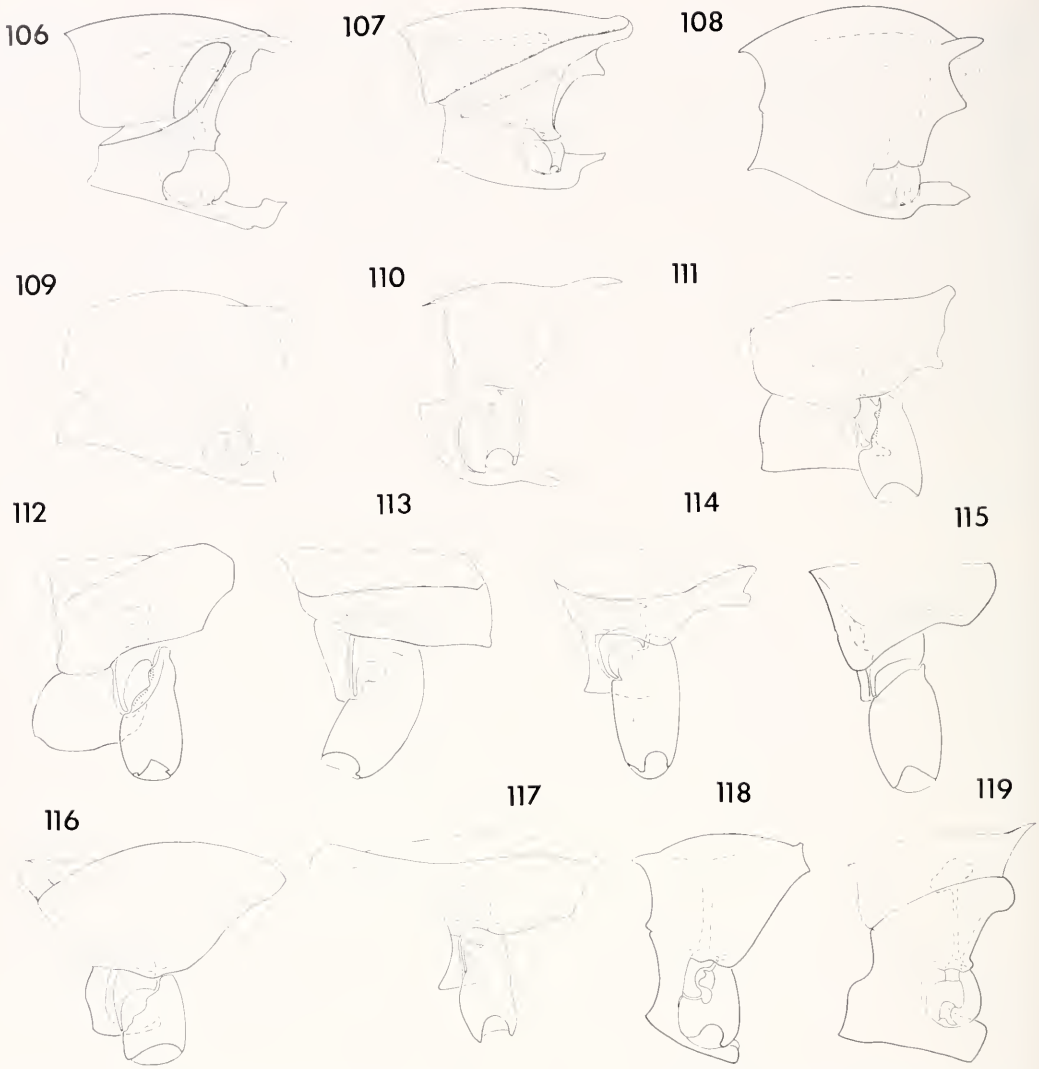
PEROTHOPIDAE
Figure 108

Elareroidea with the endopleuron solidly fused to the notal wall.

ELATERIDAE
Figure 109

High to very high volume configurations with slight variation in the degree of trochantinal reduction. Pleuron always fused at notopleural joint and sometimes against the dorsal notal wall as well.

Elements of the interlocking mechanism of other elateriforms are modified into the intersegmental articulations of the click mechanism of elaterids, see above and Figures 159–161. In preclick position, a notch near the tip of the sternal projection is placed on the rim of the mesosternal fossa, thereby creating a wide ventral gap and exposing membrane between segments. Strong articulations between the dorsal rim of the pronotum and the mesothorax-elytra form a fulcrum resulting in dorsal arching of the prothorax above the elytral plane, as the sternal projection slides forward. These dorsal articulations are formed primarily by the insertion of paired dorsal notal condyles into cavities and by placement of ridges into elytral concavities, e.g., (Fig. 159 MCnd, R.). Dorsal arching is made possible through clearances formed by sharp ventral sloping of contiguous pro- and mesothoracic surfaces and through dorsoventral compression of the posterior notal face. The click or jumping mechanism of elaterids has then evolved from the defensive promesothorax interlocking system of related forms. The click mechanism is doubtless a defense adaptation as well, but a dynamic one, working by violently rapid body movements and serving to either startle or to



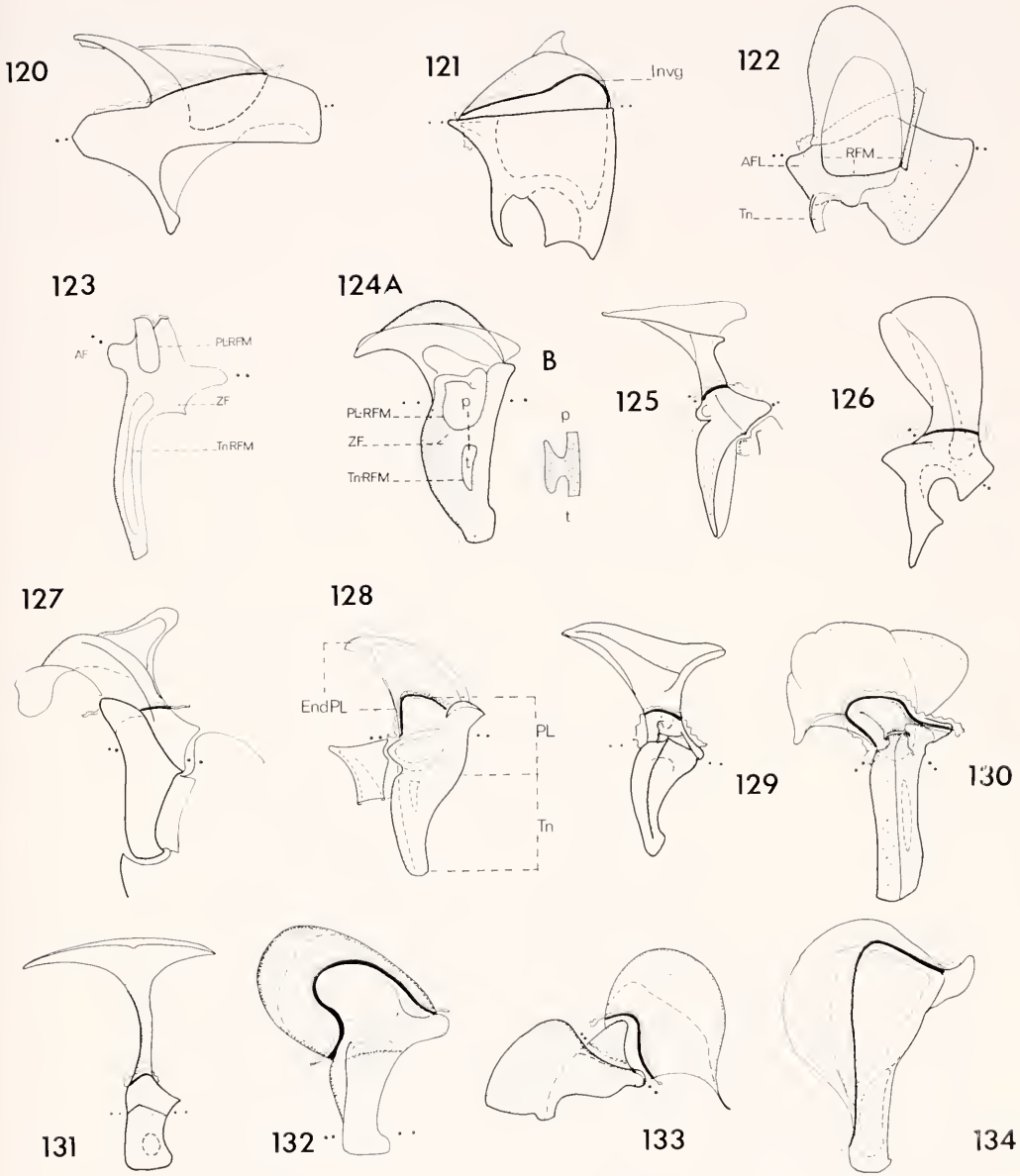
Figures 106–119. Elateroidea, Cantharoidea, Buprestoidea. 106. *Drapetes* sp. 107. *Fornax bicolor*. 108. *Perothops muscida*. 109. *Cardiophorus gagates*. 110. *Scaptolenus* sp. 111. *Homalisus fontisbellaquei*. 112. *Drilus flavescens*. 113. *Podabrus* sp. 114. *Zarhipis integripennis*. 115. *Telegeusis* sp. 116. *Eros aurora*. 117. *Photinus pyralis*. 118. *Schizopus laetus*. 119. *Acmaeodera gibbula*.

mechanically break free from predators. The latter effect is aided by a rather streamlined, hard-to-grab body contours, and by smooth or silky cuticular surfaces.

CANTHAROIDEA
Figures 111–117

Terminal elements of a malacodermization sequence, or series of sequences, resulting in reduced structural integrity, exposure of membrane, and a high degree of coxal flexation. Prothoracic structure and mechanics effected by flattening of the body in a few groups.

Sternum, promesothoracic joint, and trochantinal enclosure least modified in *Homalisus* (Fig. 111). Elongate coxae extend far below the sternum and flex in a



Figures 120–134. Pleura, Myxophaga, Polyphaga, mostly external views. 120. *Sphaerius politus*. 121. *Hydroscapha natans*. 122. *Lepicerus horni*, internal view. 123. *Sarabandus robustus*, basal aspect, internal view. 124A. *Anthobium pothos*, internal view; B. section through p-t. 125. *Prionocyphon limbatus*. 126. *Eucinetus infumatus*. 127. *Peltastica tuberculata*. 128. *Proteinus sulcatus*. 129. *Lyrosoma opaca*. 130. *Nicrophorus* sp. 131. *Catopocerus* sp. 132. *Philonthus cyannipennis*. 133. *Lathrobium prahae*. 134. *Lichnanthe vulpina*. Endopleural invagination (Invg) indicated by heavy line below sinuous membrane. Level of notal rim indicated by a pair of dots on either side of the pleuron.

nearly vertical plane in phengodids, cantharids, drilids. In flattened groups (lycids, most lampyrids) the squat coxae do not extend far below the sternum and the flexation plane is inclined sharply away from the vertical, and in some the notum is developed anteriorly to cover the hypognathous head and proleg.

BUPRESTOIDEA

Figures 118–119, 135

Rigid-body forms with a uniformly specialized pleurocoxal mechanism. Pleuron rigidly fused to notum; endopleuron with an elongate, stalklike base and a relatively small, expanded apex which comes close to the notal wall. Coxal articular region, quite small in schizopines (Fig. 118), even further reduced in buprestids, never enclosed (Figs. 119, 135).

MATERIAL EXAMINED

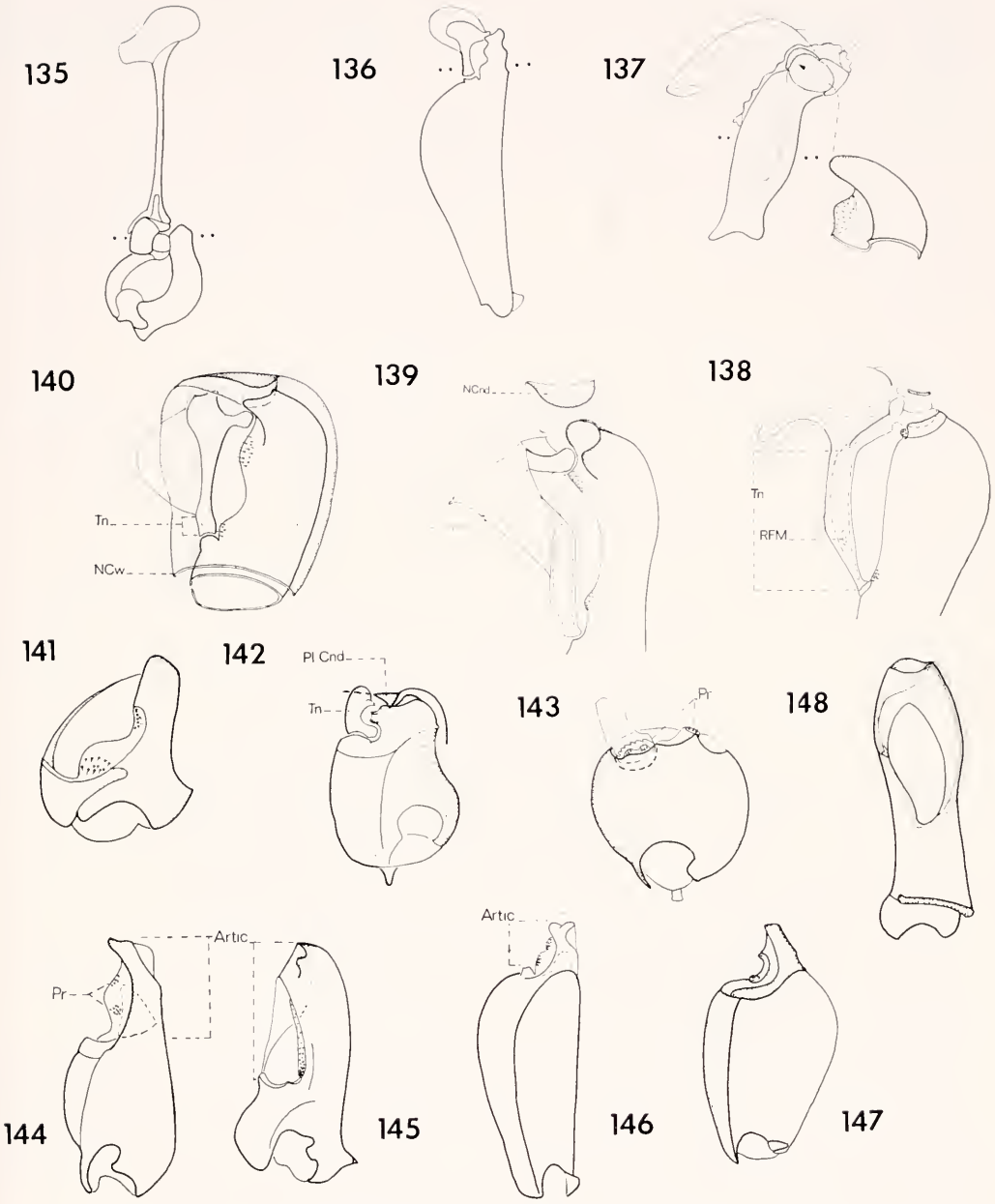
Suborder **ARCHOSTEMATA**

CUPEDIDAE
- Ommadinae
  - Ommadini, *Omma stanleyi* (Fig. 4).
  - Tetraphalerini, *Tetraphalerus wagneri* (Fig. 3).
- Cupedinae
  - Priacmini, *Priacma serrata* (Fig. 1, 141).
  - Cupedini, *Cupes concolor* (Fig. 2), *Prolixocupes lobiceps.*

MICROMALTHIDAE *Micromalthus debilis* (Fig. 5).

Suborder **ADEPHAGA**

CARABIDAE
- Carabini, *Carabus nemoralis* (Figs. 8, 149–152), *Calosoma calidum*, *Ceroglossus* sp., *Pamborus guerini.*
- Cychrini, *Sphaeroderus canadensis.*
- Nebriini, *Nebria* sp., *Leistus ferruginosus*, *Pelophila borealis.*
- Opisthiini, *Opisthius richardsoni.*
- Notiophilini, *Notiophilus semistriatus.*
- Hiletini, *Hiletus* (= *Camaragnathus*) *versutus.*
- Trachypachidini, *Trachypachus gibbsi*, *Systolosoma brevis.*
- Gehringiini, *Gehringia olympica.*
- Ozaenini, *Metrius contractus* (Figs. 10, 157), *Mystropomus regularis*, *Ozaena elevata* (Fig. 11), *Tropopsis marginicollis*, *Pachyteles* sp.
- Paussini, *Protopaussus bakeri*, *Megalopaussus amplipennis*, *Carabidomemmus pallidus*, *Homopterus bolivianus*, *Arthropterus brevis*, *Cerapterus lafertei*, *Pleuropterus alternans*, *Pentaplatartarus gestroi*, *Platyrhopalopsis mellvi*, *Paussus* sp. (Fig. 12).
- Omophronini, *Omophron ovale.*
- Cicindelini, *Cicindela rapanda.*
- Megacephalini, *Omus dejeani*, *Platychila pallida.*
- Ctenostomini, *Ctenostoma* sp.
- Collyrini, *Tricondyla* sp.
- Rhysodini, *Rhysodes hamatus*, *Clinidium* sp.
- Loricerini, *Loricera pilicornis.*
- Promecognathini, *Promecognathus laevissimus.*
- Enceladini, *Enceladus* sp.
- Saigonini, *Saigonum* sp.
- Scaritini, *Scarites substriatus*, *Clivinia impressifrons* (Fig. 9), *Ardistomis viridis.*
- Apotomini, *Apotomus* sp.
- Nomiini, *Nomius pygmaeus.*
- Broscini, *Zacotus matthewsi.*
- Psydrini, *Psydrus piceus.*
- Trechini, *Trechus loculentus.*
- Bembidini, *Bembidion putrule.*
- Pogonini, *Pogonus texanus.*
- Patrobini, *Patrobus longicornis.*
- Morionini, *Morion monilicornis.*
- Pterostichini, *Pterostichus adnoxus.*
- Lachnophorini, *Ega sallei.*
- Harpalini, *Harpalus pleuritidus.*
- Licinini, *Rembus assimilis.*
- Peleciini, *Pelecium* sp.
- Cyclosomini, *Cyclosoma flexosus.*



Figures 135–148. Pleuro-coxal Mechanisms. 135–136. Pleuron and coxa, Lateral views; 135. *Acmeodera gibbula*, 136. *Philonthus cyannipennis*, 137–140. Pleuro-coxal articulation, Histeroidea, Scarabaeoidea, Lateral Views; 137. *Sphaerites politus*, pleuron and coxal apex, 138. *Saprinus pennsylvanicus*, 139. *Hister sulcatus*, 140. *Phyllophaga* sp., notal cowling considered transparent. 141–148. Coxae, mostly lateral views; 141. *Priacma serrata*, 142. *Amphizoa insolens*, 143. *Helluomorphoides texana*, 144. *Trigonurus crotchii*, 145. *Leptochirus* sp., 146. *Philonthus cyannipennis*, 147. *Prionochaeta opaca*, 148. *Phyllophaga* sp. internal view.

Panagaeini, *Panagaeus fasciatus.*
Anthiini, *Anthia biguttata.*
Chlaenini, *Chlaenius pennsylvanicus.*
Ctenodactylini, *Leptotrachelus dorsalis.*
Odacanthini, *Colliuris pennsylvanicus.*
Masoreini, *Tetragonoderus fasciatus.*
Pentagonicini, *Pentagonica nigricollis.*
Lebiini, *Lebia grandis.*
Zuphiini, *Zuphium americanus.*
Dryptini, *Geleritula* sp.
Agrini, *Agra* sp.
Helluonini, *Helluomorphoides texana* (Figs. 143, 153–156).
Brachinini, *Brachinus janthinipennis.*
Pseudomorphini, *Sphallomorpha* sp., *Adelotopus dytiscoides.*

AMPHIZOIDAE, *Amphizoa insolens* (Figs. 7, 142, 158).
HALIPLIDAE, *Haliplus* sp., *Peltodytes* sp.
HYGROBIIDAE, *Hygrobia* sp.
DYTISCIDAE
Laccophilinae, *Laccophilus* sp.
Colymbetinae, *Agabus striatus* (Fig. 6).
GYRINIDAE
Enhydrinae, *Dineutes* sp.
Gyriniinae, *Gyrinus* sp.

Suborder **MYXOPHAGA**

SPHAERIIDAE, *Sphaerius politus* (Figs. 13, 120).
HYDROSCAPHIDAE, *Hydroscapha natans* (Figs. 14, 121).
LEPICERIDAE, *Lepicerus horni* (Figs. 15, 122).
TORRIDINICOLIDAE, *Hintonia* (= *Ptyopteryx*) *britskii* (Fig. 16), *Ytu artemis.*

Suborder **POLYPHAGA**

EUCINETOIDEA

EUCINETIDAE
Eucinetus infumatus (Figs. 22, 126), *Euscaphurus saltator.*
CLAMBIDAE
Clambus gibbosus (Fig. 24), *Sphaerothorax* sp., *Loricaster* sp. (Fig. 25), *Calyptomerus* sp. (Fig. 166), undescribed genus and species (Fig. 23).

HELODIDAE
Atopidinae, *Atopida castanea, Veronatus tarsalis.*
Helodinae, *Prionocyphon limbatus* (Figs. 21, 125), *Sarabandus robustus* (Fig. 123), *Cyphon coracinus.*

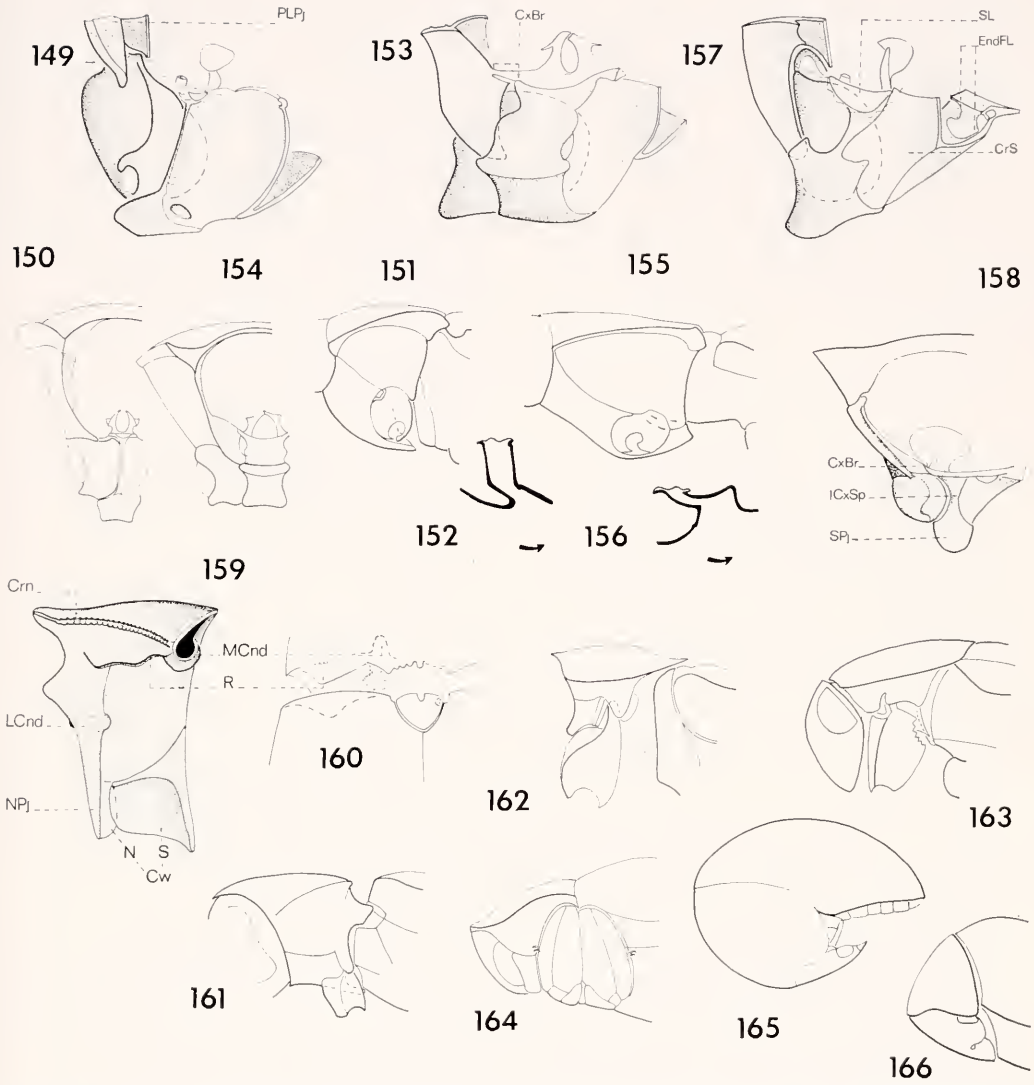
DERODONTOIDEA

DERODONTIDAE
Derodontus maculatus (Fig. 19), *Peltastica tuberculata* (Figs. 18, 127), *Laricobius rubidus* (Fig. 17), *Nothoderodontus gourlayi* (Fig. 20).

STAPHYLINOIDEA

LEIODIDAE
Glacicavicolinae, *Glacicavicola bathyscioides* (Fig. 33).
Catopocerinae, *Catopocerus* sp. (Figs. 26, 131).
Leiodinae, *Anisotoma globosa, Hydnobius matthewsi* (Fig. 27), *Agathidium* sp. (Figs. 31, 165), *Anisotoma polita* (Fig. 29).
Scotocryptinae, *Parabystus inquilinus.*
Camiarinae, *Camiarus* sp. (Fig. 28), *Neocamiarus* sp.
Coloninae, *Colon* sp.
Ptomaphaginae, *Ptomaphagus cavernicola.*
Nemadinae, *Nemadus* sp.
Catopinae, *Prionochaeta opaca* (Figs. 30, 147, 163); *Catops alsiosus.*
Bathysciinae, *Astagobius angustatus* (Fig. 32), *Leptodirus* sp., *Platycholeus leptinoides.*

SILPHIDAE
Agyrtinae
Necrophilini, *Necrophilus hydrophiloides* (Fig. 40).
Agyrtini, *Agyrtes longulus, Pelatines latus.*
Pterolominae



Figures 149–166. Intersegmental Attachments. Figs. 149–157. Pro-mesothoracic Joint of Adephaga. Figs. 149–152. *Carabus nemoralis*. 149. Postero-ventral aspect of prothorax, right coxa removed; postero-medial view of parasagittal section. 150. Lateral view of prothorax and adjacent tagmata. 151. Posterior view of prothorax parasagittal section. 152. Section through midline of prosternal projection and rim of mesosternum; arrow indicates mode of overlap as the entire prothorax moves downwards. Figs. 153–156. *Helluomorphoides texana*; sequence as in Figs. 149–152. 157. *Metrius contractus*, view as in Fig. 149. 158. *Amphizoa insolens*, view as in Fig. 151. Figs. 159–161. *Ptilodactyla serricollis*, promesothoracic interlocking system. 159. Postero-medial view of parasagittal section of prothorax, coxa and pleuron removed. 160. Dorsal view of intersegmental attachment. 161. Lateral view. Figs. 162–166. Lateral views, various Polyphaga. 162. *Nicrophorus* sp. 163. *Prionochaeta opaca*. 164. *Chelonarium lecontei*. 165. *Agathidium* sp. 166. *Calyptomerus* sp.

Pterolomini, *Pteroloma caraboides*.
Lyrosomini, *Lyrosoma opaca* (Figs. 39, 129).
Silphinae
Silphini, *Silpha inaequalis*, *Silpha americana*.
Necrodini, *Necrodes surinamensis* (Figs. 42, 162).

Nicrophorinae, *Nicrophorus* sp. (Figs. 41, 130).
STAPHYLINIDAE
Piestinae
Trigonurini, *Trigonurus crotchii* (Figs. 46, 144).
Piestini, *Siagonium punctatum, Piestus* sp. (Fig. 48), *Apatetica* sp., *Nodynus leucofasciatus* (Fig. 47).
Empelinae *Empelus brunnipennis* (Fig. 43).
Proteininae
Proteinus sulcatus (Figs. 44, 128); *Megarthrus pictus.*
Omaliinae
Anthophagini, *Anthobium pothos* (Fig. 124), *Amphichroum testaceum, Trigonodemus striatus.*
Omaliini, *Omalium marginatus* (Fig. 45), *Phlaeopterus longipalpus.*
Oxytelinae
Oxytelini, *Oxytelus fuscipennis* (Fig. 57), *Bledius* sp. (Fig. 58).
Osoriinae
Lispinini, *Lispinus californicus.*
Leptochirini, *Leptochirus* sp. (Figs. 51, 145).
Osoriini, *Osorius stipes* (Fig. 50).
Oxyporinae, *Oxyporus lateralis* (Fig. 52).
Steninae, *Stenus juno* (Fig. 56).
Paederinae
Pinophilini, *Pinophilus picipes.*
Paederini, *Lathrobium prahae* (Figs. 53, 133).
Staphylininae
Staphylinini, *Philonthus cyannipennis* (Figs. 54, 132, 136, 146), *Thinopinus pictus, Creophilus maxillosus.*
Quediini, *Quedius fulvicollis.*
Habrocerinae, *Habrocerus capillaricornis.*
Tachyporinae
Tachyporini, *Tachinus fimbriatus* (Fig. 49).
Aleocharinae
Myrmedoniini, *Xenodusa* sp.
Aleocharini, *Aleochara lata* (Fig. 55).
MICROPEPLIDAE, *Micropeplus laticollis* (Fig. 67).
DASYCERIDAE, *Dasycerus carolinensis* (Fig. 38).
BRATHINIDAE, *Brathinus nitidus* (Fig. 34).
HYDRAENIDAE
Hydraeninae, *Hydraena pennsylvanica* (Fig. 70). *Ochthebius* sp. (Fig. 68).
Limnebiinae, *Limnebius piceus* (Fig. 69).
PTILIIDAE
Nanosellinae, *Nanosella fungi.*
Ptiliinae, *Acratrichis* sp. (Fig. 35), *Nossidium* sp. (Fig. 34).
LIMULODIDAE, *Limulodes paradoxus.*
LEPTINIDAE
Leptininae, *Leptinus testacaeus, Leptinillus validus* (Fig. 37).
Platypsyllinae, *Platypsyllus castoris.*
SCAPHIDIIDAE
Scaphidiini, *Scaphium castanipes* (Fig. 59), *Scaphidium* sp.
Scaphisomini, *Scaphisoma castaneum* (Fig. 60).
SCYDMAENIDAE
Scydmaeninae
Chevrolatiini, *Chevrolatia amoena* (Fig. 63).
Leptoscydmini, *Leptoscydmus cavifrons.*
Cephenniini, *Cephennium carporosum.*
Eutheini, *Veraphis* sp.
Euconnini, *Connophron flavicarse* (Fig. 61).
Lophioderini, *Lophioderus* sp.
Scydmaenini, *Scydmaenus perforatus.*
Eumicrini, *Eumicrus grossus.*
Clidicinae
Clidicini, *Clidicus* sp. (Fig. 62), *Leptomastix emeryi.*
Mastigini, *Mastigus dalmatinus.*
PSELAPHIIDAE
Faroninae
Faronini, *Sonoma tulnae* (Fig. 64).
Pselaphinae
Euplectini, *Euplectus confluens.*
Tmesiphorini, *Tmesiphorus costalis* (Fig. 65).
Clavigerinae
Fustigerini, *Fustiger fuchsi* (Fig. 66).

HYDROPHILOIDEA

HYDROPHILIDAE
- Sphercheinae, *Spercheus* sp. (Fig. 71).
- Helophorinae, *Helophorus* sp. (Fig. 75).
- Epimetopinae, *Epimetopus costatus* (Fig. 73).
- Hydrochinae, *Hydrochus callosus.*
- Hydrophilinae, *Hydrophilus triangularis, Tropisternus lateralis, Hydrochara* sp.
- Berosinae, *Berosus striatus.*
- Hydrobiinae, *Sperchopsis tesselatus, Enochrus pygmaeus nebulosus* (Fig. 74), *Helobata striata.*
- Chaetarthriinae, *Chaetarthria* sp.
- Sphaeridiinae, *Sphaeridium scarabaeoides.*

GEORYSSIDAE
- *Georyssus californicus* (Fig. 72).

HISTEROIDEA

SPHAERITIDAE
- *Sphaerites politus* (Figs. 76, 137).

SYNTELIIDAE
- *Syntelia mexicana* (Fig. 77).

HISTERIDAE
- Saprininae, *Saprinus pennsylvanicus* (Fig. 138).
- Histerinae, *Hister sulcatus* (Figs. 78, 139), *Hololepta fossularis.*

SCARABAEOIDEA

LUCANIDAE
- Syndesinae, *Ceruchus piceus* (Fig. 80).
- Lucaninae, *Pseudolucanus capriolus.*

PASSALIDAE
- Pseudacanthinae, *Popilius disjunctus* (Fig. 81).

SCARABAEIDAE
- Scarabaeinae, *Copris fricator* (Fig. 82), *Dichotomius* (= *Pinotus*) sp.
- Aphodiinae, *Aphodius* sp.
- Chironinae, *Chiron* sp.
- Pleocominae, *Pleocoma* sp. (Fig. 79), *Acoma brunnea.*
- Glaphyrinae, *Lichnanthe vulpina* (Fig. 134).
- Ochodaerinae, *Ochodaeus biarmatus.*
- Ceratocanthinae, *Cloeotus globosus.*
- Troginae, *Trox gemmulatus.*
- Geotrupinae, *Geotrupes semiopacus.*
- Rutelinae, *Anomala binotata.*
- Melolonthinae, *Phyllophaga* sp. (Figs. 83, 140, 148).
- Dynastinae, *Bothynus* sp.
- Trichiinae, *Osmoderma* sp., *Gnorimella maculosa*
- Cetoniinae, *Euphoria lambalis* (Fig. 84).

ELATERIFORMIA

ARTEMATOPOIDEA

ARTEMATOPIDAE, *Artematopus puncticollis* (Fig. 90).
- *Eurypogon niger* (Fig. 89), *Macropogon testaccipennis.*
- *Macropogon villosus, Allopogonia villosus.*

BRACHYPSECTRIDAE, *Brachypsectra fulva* (Fig. 87).

CEROPHYTIDAE, *Cerophytum elateroides* (Fig. 88).

DASCILLOIDEA

DASCILLIDAE
- Dascillinae, *Dascillus davidsoni* (Fig. 85), *D. cervinus, D. plumbeus.*
- Karumiinae, *Anorus piceus, A. arizonicus, Karumia estafilinoides.*

RHIPICERIDAE, *Sandalus niger* (Fig. 86), *Rhipicera marginata, Arrhaphipterus sckelkownikoffi.*

BYRRHOIDEA

BYRRHIDAE
- Byrrhinae.
- Amphicyrtini, *Amphicyrta chrysomelina, Lioon speculara.*
- Simplocarini, *Simplocaria tessellata.*
- Morychini, *Morychus subsetosus.*
- Byrrhini, *Byrrhus americanus* (Fig. 91), *Cytilus* sp.

Pedilophorini, *Listemus acuminatus*, *Pedilophorus* sp.

SYNCALYPTINAE
Syncalypta spinosa. *Curimopsis* sp., *Microchaetes* sp.

DRYOPOIDEA

PTILODACTYLIDAE
Anchytarsinae, *Anchytarsus bicolor*, *Anchycteis velutina* (Fig. 102), *Odontonyx trivittis*, *Araeopidius monachus* (Fig. 103), *Octoglossa* sp., *Paralichas guerni*, *Epilichas atricolor*, *Therius suturalis*.
Eulichadinae(idae), *Eulichas mus*, *Stenocolus scutellaris* (Fig. 100).
Ptilodactylinae, *Ptilodactyla serricollis* (Figs. 104, 159–161), *Lachnodactyla arizonica*, *Chaetodactyla lyciformis*.
CHELONARIIDAE, *Chelonarium lecontei* (Figs. 105, 166), *Chelonarium* spp.
CALLIRHIPIDAE, *Zenoa picea* (Fig. 101), *Horatocera nipponica*, *Callirhipis* sp.
PSEPHENIDAE
Psepheninae, *Psephenus* spp. (Fig. 95), *Mataeopsephus* sp., *Pheneps gracilis*.
Eubrianacinae, *Eubrianax edwardsi* (Fig. 93).
Eubriinae, *Ectopria nervosa*, *Acneus 4-maculatus*, *Eubria palustris*, *Sclerocyphon* sp., *Dicranopselaphus* sp. (Fig. 94), *Tychepsephus felix*, *Schinostethus* sp.
HETEROCERIDAE
Auglyini, *Auglyles auromicans*.
Tropicus, *Tropicus pusillus*.
Heterocerini, *Heterocerus pallidus* (Fig. 92).
LIMNICHIDAE
Limnichinae, *Eulimnichus analis*, *Limnichites nebulosus*, *Byrrhinus* sp., *Limnichus analis*.
Bothriophorinae, *Physemus minutus*.
Cephalobyrrhinae, *Throscinus* sp.
Thaumastodinae, *Martinius ripisaltater*, *Pseudoeucinetus* sp.
Lutrochinae, *Lutrochus geniculatus* (Fig. 96).
DRYOPIDAE, *Helichus fastigiatus*, *Pelonomus obscurus* (Fig. 99); *Dryops arizonensis*.
ELMIDAE
Larinae
Larini, *Lara amphipennis* (Fig. 97).
Potamophilini, *Potamophilus* spp.
Elminae
Elmini, *Stenelmis crenata* (Fig. 98).
Ancyronychini, *Ancyronyx variegatus*.

ELATEROIDEA

CEBRIONIDAE, *Selonodon bicolor*, *Scaptolenus* sp. (Fig. 110), *Cebrio gigas*, *Euthysanius laurus*, *Aplastus piceicollis*, *Octinodes megalops*.
THROSCIDAE
Throscinae, *Aulonothroscus* sp., *Trixagus* spp., *Pactopus horni*.
Lissominae, *Lissomus bicolor*, *Drapetes* sp. (Fig. 106).
Balginae, *Cussolenis mutabilis*, *Thylacosternus* sp.
EUCNEMIDAE
Melasinae, *Melasis rufipennis*, *Cryptosoma* sp., *Isorhipis ruficornis*, *Anelastes druryi*, *Palaeoxenus dohrni*.
Dirhaginae, *Dirhagus triangularis*.
Gastraulacinae, *Gastraulacus* sp.
Eucneminae, *Fornax bicolor* (Fig. 107), *Pterotarsus* sp.
PEROTHOPIDAE, *Perothops mucida* (Fig. 108).
ELATERIDAE
Pyrophorinae, *Alaus* spp., *Chalcolepidius* sp.
Elaterinae, *Pityobius anguinus*, *Ctenicera* sp., *Agriotes* sp.
Melanactinae, *Melanactes piceus*.
Oestodinae, *Oestodes tenuicollis*.
Negastrinae, *Negastrinus belumbis*.
Hypolithinae, *Athous* sp.
Adrastinae, *Glyphonyx testaceus*.
Melanotinae, *Melanotus* spp.
Cardiophorinae, *Cardiophorus gagates* (Fig. 109).

CANTHAROIDEA

HOMALISIDAE, *Homalisus fontisbellaquei* (Fig. 111).
DRILIDAE, *Drilus flavescens* (Fig. 112), *Selasia* sp.
TELEGEUSIDAE, *Telegeusis* sp. (Fig. 115).
PHENGODIDAE, *Phengodes* spp., *Zarhipis integripennis* (Fig. 114).
Mastinocerus sp.
LAMPYRIDAE
Lampyrinae, *Lamprocera* sp., *Pleotomus pallens*.
Photinus pyralis (Fig. 117), *Lucidota punctata*.
Photurinae, *Photurus* sp.
Luciolinae, *Luciola* sp.
Pterotinae, *Pterotus obscuripennis*.
Rhagophthalminae, *Ochotyra semiusla*.
CANTHARIDAE
Chauliognathinae. *Chauliognathus pennsylvanicus*.
Cantharinae, *Podabrus* sp. (Fig. 113).
Cantharis sp., *Malthodes* sp.
LYCIDAE
Lycini, *Lycus* sp.
Calopterini, *Calopteron* sp.
Dictyopterini, *Eros aurora* (Fig. 116).
Platerodini, *Plateros modestus*.

BUPRESTOIDEA

SCHIZOPODIDAE, *Schizopus laetus* (Fig. 118), *Dystaxia elegans*.
Glyptoscelimorpha marmorata
BUPRESTIDAE
Julodinae, *Sternocera pulchra*.
Acmaeoderinae, *Acmaeodera gibbula* (Figs. 119, 135).
Buprestinae, *Dicerca divaricata*.
Agrilinae, *Brachys tesselata*.

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The Fossil Aardvarks (Mammalia: Tubulidentata)

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THE FOSSIL AARDVARKS (MAMMALIA: TUBULIDENTATA)

BRYAN PATTERSON[1]

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ABSTRACT. A new tubulidentate, *Leptorycteropus guilielmi* gen. et sp. nov. from Member B of Lothagam–1, Turkana District, Kenya, is described. It is a generalized form for an aardvark, despite its relatively recent age. Review of the known fossils indicates that *Leptorycteropus, Orycteropus* and *Myorycteropus* are representatives of three phyletic lineages. The aberrant Malagasy *Plesiorycteropus* is so distinct from the rest as to suggest that its ancestors reached the island at some time during the Eocene. A division of the family Orycteropodinae into Orycteropodinae and Plesiorycteropodinae nov. is proposed. The biology of *O. afer* and the nature of the myrmecophagous adaptation are reviewed, and the possible adaptations of the extinct genera discussed. The surviving species, as a fully committed myrmecophage, is anomalous in retaining functional posterior cheek teeth, a retention that may be related to the curious symbiosis between this animal and the cucurbitaceous plant *Cucumis humifructus*. Available evidence is consistent with the hypotheses of condylarth-tubulidentate relationships and of Africa as the place of origin of the aardvarks.

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INTRODUCTION

Among the fossil vertebrate remains collected in the Pliocene deposits at Lothagam Hill, Turkana, Kenya, during the field season of 1967 was a partial skeleton of an extinct aardvark that had evidently served as a meal for some carnivore. Several of the bones show tooth punctures, and the parts preserved are such as would remain after predator action. I am obliged to this otherwise unknown animal. Study of the surviving portions of its repast revealed the existence of the most generalized member of a peculiar and interesting order so far found and led to this review.

Our field work in East Africa was supported by National Science Foundation Grants GP–1188 and GA–425. For the privilege of examining material in the British Museum (Natural History) and the Muséum Nationale d'Histoire Naturelle I am indebted to Mrs. Shirley Coryndon Savage, Dr. A. J. Sutcliff, Dr. J.-P. Lehman and Dr. R. Hoffstetter. Figures 14 and 15 have been drawn by Mr. Laszlo L. Mészöly from sketches by me; the remainder are by Mr. Arnold Clapman.

TUBULIDENTATA

ORYCTEROPODIDAE

Orycteropodinae (see p. 216)

Leptorycteropus[1] gen. nov.

Type species. — *L. guilielmi*[1] sp. nov.

Diagnosis. $1\frac{?}{?}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$. Canines oval in section, larger than premolars; canines and premolars with peripheral ring of cement; known molars comparable in size and structure to those of *Orycteropus*, large relative to size of animal. Maxillaries not extending forward to form elongate snout, not notched anteriorly, ventral surface of palatal portion flat, not grooved medially; anterior portion of jugal wider, relatively shallower than in *Orycteropus*, forming, with maxillary, a short, blunt descending process; dorsal portion of frontoparietal suture more oblique than in *Orycteropus*; symphysis of mandible extending back to level of anterior end of $P_{\overline{2}}$. Centra of presacral vertebrae generally wider relative to depth than in *Orycteropus*, sacrals five. Limb bones in general more slenderly constructed than in *Orycteropus*, especially in shafts; much narrower across distal extremities than in *Myorycteropus*. Humerus with deltoid crest merging into shaft distally, not forming distinct terminal projection, no large V-shaped deltopectoral area, entepicondyle extending as far distally as trochlea; anteroposterior diameter of distal end of radius short relative to transverse. Pectineal process of ilium much less projecting than in *Orycteropus*; medial surface of ischium very concave dorsal to obturator foramen. Hind leg bones more slenderly constructed than in *Orycteropus*.

Distribution. Pliocene, East Africa.

[1] λεπτός, slender + *Orycteropus*; in allusion to the comparatively slender limb bones. The species is named for Dr. William D. Sill, finder of the type specimen.

Leptorycteropus guilielmi sp. nov. (Figures 1–9)

Type. In Kenya National Museum, M.C.Z. Field No. 94–67K, various fragments of the skeleton of a single, adult individual: anterior portion of right maxilla with broken C and P^{1-2}; posterior portion of right maxilla with broken M^{2-3} and posterior extremity of alveolus of M^1; anterior root of left zygomatic arch with part of orbital rim; part of cranial roof including right postorbital process; part of left horizontal ramus with broken C– $P_{\overline{4}}$ and antero-internal part of alveolus of $M_{\overline{1}}$; several vertebrae in varying states of incompleteness: C 3–4, 6–7, an intermediate dorsal (D. 6?), D. 11–13, L. 3–8, sacrum, Cd. 1 and three other anterior caudals; a rib fragment; most of proximal and distal halves of left humerus, greater tuberosity and part of head missing; two fragments of proximal part of right humerus; distal portion of right radius, fragment of center of shaft of right ulna; distal portion of right Mc. II; pelvis lacking posterior portions of ischia and pubes, iliac crests incomplete; right femur incomplete in shaft and with head, great trochanter and external condyle missing; distal portion of left femur lacking internal condyle; proximal two-thirds and distal extremity of left tibia, proximal and distal portion of right tibia, distal portion of right fibula.

Hypodigm. Type only.

Horizon and locality. Lothagam –1, low in Member B (Patterson, Behrensmeyer and Sill, 1969), Pliocene; Lothagam Hill, southeastern Turkana, Republic of Kenya.

Diagnosis. As for the genus; approximately half the size of *Orycteropus afer*.

Dentition. The maxillary and mandibular fragments combine to reveal that a canine and the normal eutherian complement of cheek teeth were present; the specimen provides no information as to the presence or absence of incisors. $P\frac{1}{1}$ are separated from the canines and $P\frac{2}{2}$ by short diastemata, and the rest of the cheek teeth

are set off from each other by small gaps comparable to those occurring in *Orycteropus* and *Myorycteropus*. All teeth show tubular[1] structure. The tubes increase in size from the canines backward and also, particularly in the molars, from the centers to the peripheries of the teeth. Canines and premolars have a continuous peripheral ring of cement[2]; in this feature they closely resemble the sections of the last lower milk molar of *O. afer* figured by Thomas (1890). The ring is thin in $P_{\overline{4}}$ and evidently not present in $M^{\underline{2-3}}$.

The upper canine is oval in contour, wider and slightly longer than any of the premolars preserved, either upper or lower. Of the lower canine only the posterior extremity is present. $P^{\underline{1}}_{\overline{1}}$ are the smallest of the cheek teeth and are rather wider relative to length than the narrow, elongate-oval $P^{\underline{2}}_{\overline{2-3}}$. $P_{\overline{4}}$ is wider posteriorly than its predecessors. What remains of the alveoli of $M^{\underline{1}}_{\overline{1}}$ suggests that the size difference between premolars and molars was at least as pronounced as in *Orycteropus* and perhaps more so. $M^{\underline{2-3}}$ are similar to the corresponding teeth of the living species, both in size and structure. The two lobes of $M^{\underline{2}}$ are approximately equal, the labial groove is deeper than the lingual, the anterior face is flat and the posterior rounded. $M^{\underline{3}}$ is broadly oval in outline with only a vestige of the labial groove present.

Skull. The anterior part of the right maxilla includes the palatal portion as far as the median suture. This fragment shows that the bony palate was flat transversely and very slightly concave anteroposteriorly, did not have a median groove, and was not notched anteriorly for the reception of processes of the premaxillae. The surface of the bone is to a slight and irregular degree undulating, and is perforated by a large number of minute vascular openings. It is probable that a palatal exposure of the vomer was lacking. The facial portion of the bone displays a degree of curvature

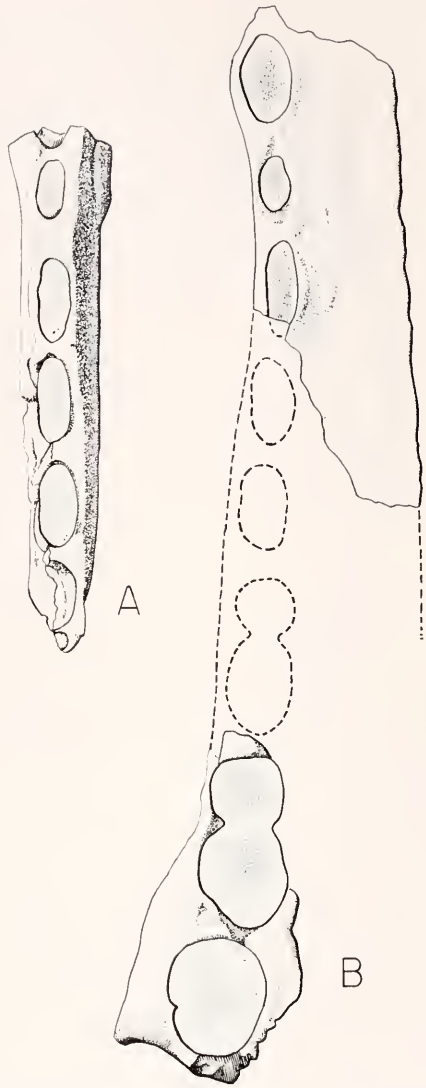


Figure 1. *Leptorycteropus guilielmi* gen. et sp. nov. Dorsal view of portions of left ramus (A) and of right maxilla (B). All teeth are broken and have been restored in the drawings to the alveolar level. × 3/2.

[1] MacInnes (1956, 9.8), pointing out that tubule, in dental terminology, is universally used for the minute canals that enter the dentine from the pulp cavity, prefers column or pillar as a name for the macroscopically visible structures. However, these are literally tubes of dentine enclosing cores of pulp and it would seem possible, within the context of the Tubulidentata, to use both tube and tubule without confusion, even though the adjectival forms of both are the same.

[2] Confirmed by the preparation of sections.

Figure 2. *Leptorycteropus guilielmi* gen. et sp. nov. Dorsal view of portion of cranial roof. ×3.

similar to that of *Orycteropus*. There was no prolongation into a long snout. The posterior portion of the maxilla is large relative to the size of the animal; the anterior root of the zygoma arises as far above $M^{\overline{3}}$ as does that of some specimens of *O. afer*. The root is more massively constructed than in *Orycteropus*, but the jugal is not as deep in this area. With the maxillary, it forms a short, blunt descending process; between this and the sidewall of the maxillary there is a long, wide and shallow groove. The postorbital process is also about as large as specimens of the living species and is similarly rugose above. Part of the frontoparietal suture is preserved; its decidedly oblique course on the cranial roof shows that the frontals extended back between the parietals to a greater extent than in *Orycteropus*. These few pieces show that the proportions of the skull were different from those of the surviving form.

The ramus of the mandible between C and $M_{\overline{1}}$ is laterally compressed, relatively deep, and, in profile, very slightly convex above and concave below. A single mental foramen is present beneath $P_{\overline{2}}$; a well-marked groove runs forward from it. On the lateral face the beginning of a swelling is preserved at the level of the posterior extremity of the canine. The ventral half of the anterior end of the medial surface is thickened, slightly rugose and grooved anteroposteriorly. This can only be a part of the symphysis; it ends posteriorly beneath the anterior extremity of $P_{\overline{2}}$ and is much deeper and more solidly constructed than that of *Orycteropus*.

Vertebrae. The vertebrae preserved closely resemble those of *Orycteropus*. Nothing indicates that the curvature of the column was appreciably different. What remains of the neural spines of D. 6(?) and of the last three dorsals suggests that the spine of the former vertebra was inclined posteriorly to a similar degree and that the anticlinal vertebra was the penultimate dorsal. The last six lumbars are present and the differences between the anterior

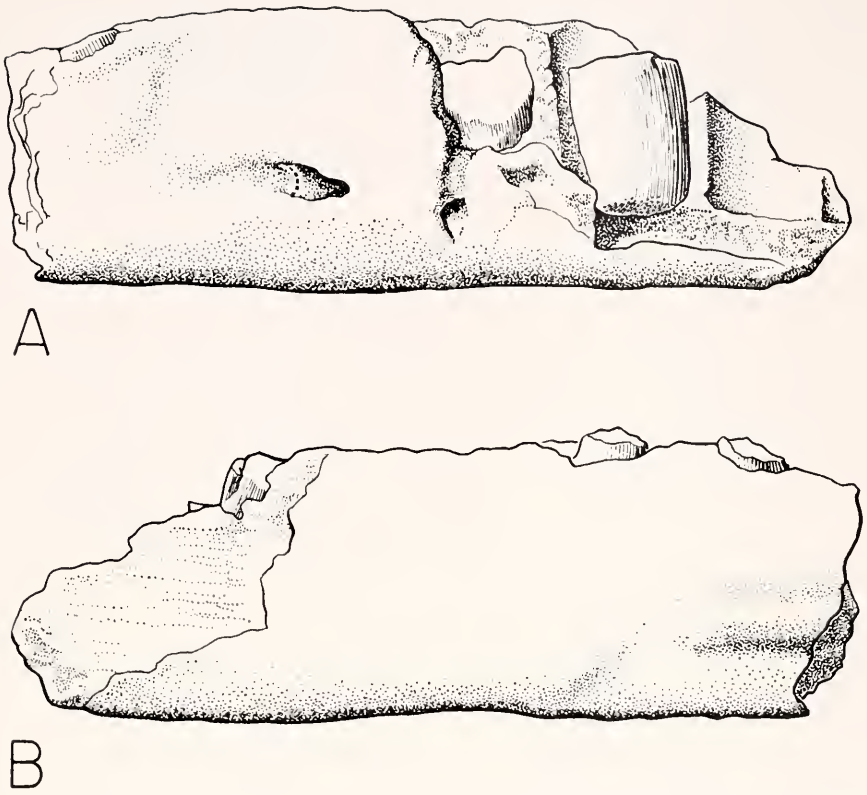


Figure 3. *Leptorycteropus guilielmi* gen. et sp. nov. Lateral, A, and medial, B, views of portion of left ramus. × 3.

of these and the last dorsal would require more than one vertebra to bridge the gap. The trunk formula was therefore probably the same, namely D. 13, L. 8. The caudal vertebrae are proportionally as large.

The presacral vertebrae differ consistently from those of *Orycteropus* in having flatter centra that are shallower dorsoventrally relative to their widths, and in having the pedicles less notched posteriorly. No doubt other minor differences between the two would be apparent were those vertebrae better preserved, but almost all of them have all processes broken off. The left metapophysis of L. 6 is in fact the only nearly complete one present; it differs from the corresponding process of *Orycteropus* in being more vertically directed, relatively higher and less expanded dorsally. Other distinctions detected are: the dorsal portion of the transverse process of C. 6 rises more ventrally[1]; the base of the transverse process of D. 6(?) is narrower anteroposteriorly, oval in section with the long axis dorsoventral; the anapophyses of D. 11–12, to judge from the remains, were longer and more slender; and the hypapophyses of L. 4–5 are relatively deeper. Colbert (1941: 322) pointed out that the zygapophyses of the lumbars of *O. gaudryi* are not as concave and convex—hence less interlocking—as those of the living species. This is like-

[1] C. 7 has no vertebrarterial canal. Sonntag (1926: 455) and Colbert (1941: 322) state that this is present in the corresponding vertebra of *Orycteropus*. It is a variable character, however, as is shown by two specimens in the museum collections that lack it.

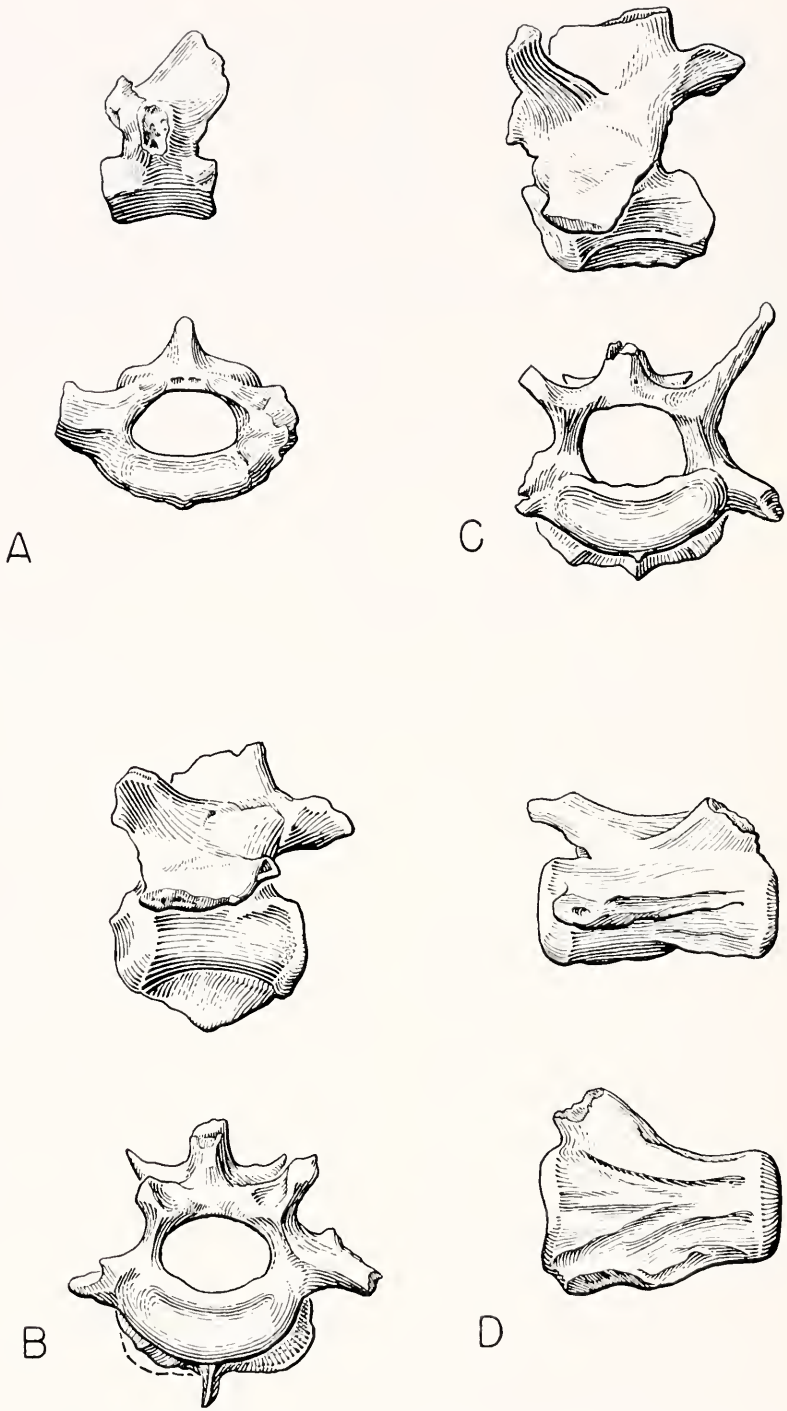


Figure 4. *Leptorycteropus guilielmi* gen. et sp. nov. Vertebrae. Left lateral and anterior views of D6? (A), L5 (B), L6 (C), left lateral and ventral views of Cd. 7 (D), ×3/2.

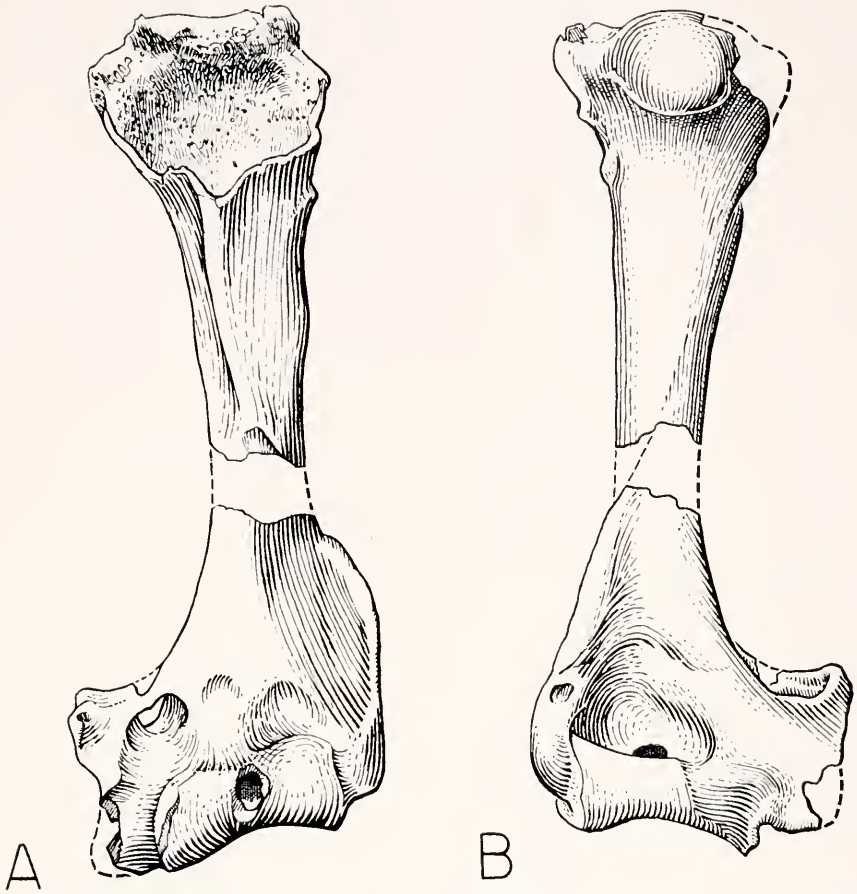


Figure 5. *Leptorycteropus guilielmi* gen. et sp. nov. Anterior (A), and posterior (B), views of left humerus. × 3/2.

wise true of *Leptorycteropus,* in which these articulations in both lumbars and posterior dorsals also do not present medially and laterally to the same degree.

Five vertebrae are incorporated in the sacrum as compared to six in *Orycteropus.* The bone is more deeply notched at the junctions of S. 3 and 4. The spines of S. 3–5 are separate at their bases. The centrum of S. 1 resembles those of the presacrals in its flatness and greater width relative to height; that of the last of the series is closer to *Orycteropus* in proportions. The bone is narrower across S. 3–4, i.e., the transverse processes of these vertebrae are relatively less expanded, and the iliac surface is conspicuously shallower dorsoventrally relative to its length than in the living form.

Insofar as comparison is possible, Cd. 1 is similar to the last pseudosacral (S. 6) of *Orycteropus.* The other three caudals preserved progressively increase posteriorly in the lengths of their centra; although other dimensions progressively decrease in the living form, the lengths of the centra remain nearly constant as far back as Cd. 12, after which a decrease begins. The transverse processes of *Leptorycteropus* arise farther back on the centrum, the neural arches are less notched anteriorly and pos-

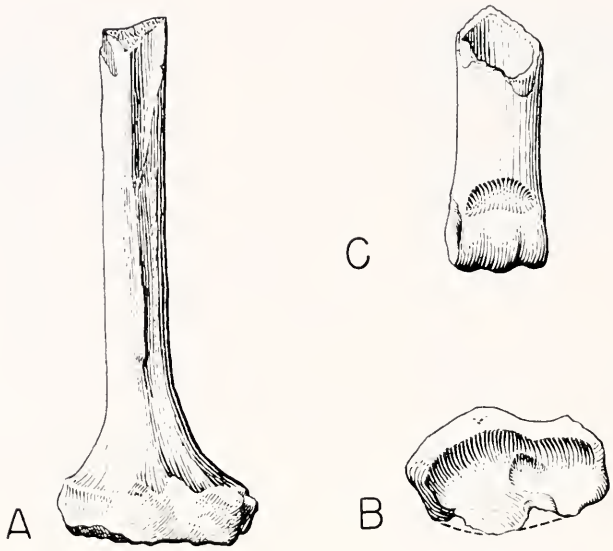


Figure 6. *Leptorycteropus guilielmi* gen. et sp. nov. Anterior (A), and distal (B), views of distal portion of right radius; anterior view (C), of distal portion of right Mc. II. ×3/2.

teriorly, and the zygapophyses are smaller than in the corresponding vertebrae of *Orycteropus*. Raised areas at the posterior ends of the ventral surfaces of the centra mark the positions of the chevron bones.

These three caudals are tentatively determined as 3, 6 and 7. Their relative order is determined by progressive decrease in the size of the bases of their transverse processes. The identification of the last of them as Cd. 7 is based on a general agreement with Cd. 6 of *Orycteropus* (S. 6 of the one being Cd. 1 of the other, and so on), the last of the series in which the neural arch extends posteriorly well beyond the centrum and the spinal nerve passes laterally through a notch. From Cd. 7 to and including Cd. 12 of *Orycteropus*, after which the neural arch disappears, the upper parts of the pedicles enlarge backward and downward to join the centrum, converting the notch into a foramen. This determination is not certain, of course, since characters such as these are subject to intra- and interspecific variation in position within the series; the vertebra of *Leptorycteropus* in question could be Cd. 8 or even perhaps Cd. 9, but not, I think, farther back than that.

Anterior extremity. A section of the shaft of the left humerus is lacking. Calculations based on what is preserved of the radius and the ratio of the radius length to the humerus length in other members of the family suggest that humeral length in *Leptorycteropus* was approximately as restored in Figure 5. The anterior part of the proximal end, including much of the head and greater tuberosity and all of the lesser tuberosity, was lost prior to burial. What remains resembles in general the corresponding part in *Orycteropus;* the depression in the lateral surface of the greater tuberosity is equally well developed in both forms. The comparatively slender shaft appears to have been straighter, less bowed than in the other genera. The deltoid crest is unique in being rather feebly developed, nearly straight and merging imperceptibly at its distal end into the body of the shaft. The pectoral crest, while strong proximally where it forms a

small shelf, is weak distally and, like the deltoid, merges into the shaft. It does not curve around onto the anterior face to contribute to a deltoid tuberosity and delimit a definite V-shaped deltoid area. Posteriorly, the shaft shows no indication of the prominent crests described by MacInnes in *Myorycteropus*. The distal end resembles that of *Orycteropus* in most features, as it is less expanded transversely than in *Myorycteropus* and has a more prominent supinator crest than in *Plesiorycteropus*. It differs from all three in the greater distal extent of the entepicondyle.

The distal three-fourths of the radius is preserved. The crest on the anterior surface resembles that of *Orycteropus* but is less salient. The crest in *Myorycteropus* is more salient distally, in *Plesiorycteropus* very greatly expanded. The distal end is shorter relative to width than in *Orycteropus* and *Plesiorycteropus*, and is much less expanded transversely than in *Myorycteropus*.

What appears to be a portion from the center of the shaft of a right ulna is all that is preserved of this bone. It is long and of even length anteroposteriorly, thin transversely, grooved laterally and gently convex medially. If correctly identified—and I can refer the fragment to no other part of the orycteropodid skeleton—*Leptorycteropus* resembled *Myorycteropus* and *Orycteropus* in the anteroposterior dimensions of the ulnar shaft and differed decidedly from *Plesiorycteropus*, in which the shaft tapers distally.

The median keel of the distal articular surface of Mc. II is blunter and less projecting than in *Orycteropus* and *Myorycteropus*; it extends to the dorsal side of the bone.

Posterior extremity. A considerable part of the pelvis is preserved, although the posterior portions of the pubes and ischia and much of the dorsal margins of the ilia are lacking. Pelvic proportions as preserved are much as in *Orycteropus*; the ischium is present as far back as the beginning of the turnout to the lateral process, and this part of the bone bears the same size relation to the ilium as does that of the living form. Unfortunately, neither in *Leptorycteropus* nor in *Myorycteropus* is there any indication as to whether or not the ischium extended as far posteriorly as in *Orycteropus*. It does not do so to any extent in *Plesiorycteropus*, in which the area of the ischial tuberosity is more compact. The marked extension in the living form, whereby the postacetabular portion of the innominate has come to equal the preacetabular in length, may be a specialization within the *Orycteropus* lineage. Ilium and ischium of *Leptorycteropus* together form a straighter line in direct acetabular view than is the case in the living form, in which the two bones slope upward from the articulation. The ilium curves laterally to about the same degree as in *Orycteropus* but is more tapered at the extremity. On the gluteal face the linea glutea inferior is sharp and more prominent, especially anteriorly, than in *Orycteropus*. The portion of the bone below it presents more ventrally. A linea glutea superior is not present on the part of the bone preserved, and was probably situated at or near the missing dorsal rim. The gluteal face is slightly less, the medial face rather more concave than in the living form. The ventral portion of the great sciatic notch is preserved, indicating that there was some posterosuperior expansion of the ilium. As the dorsal rim is broken off, it is impossible to estimate how large this may have been. I suspect that it was considerably less extensive than in *Orycteropus*. In the latter, the deep sacral articulation extends well up on to it, whereas in *Leptorycteropus* the shallower articulation does not extend beyond the part preserved; in the *Myorycteropus* material the critical area is broken off. *Plesiorycteropus* shows no trace of such a structure, the dorsal rim of the ilium flowing rather gently down to the posterior end of the sacral articulation. The large dorsal

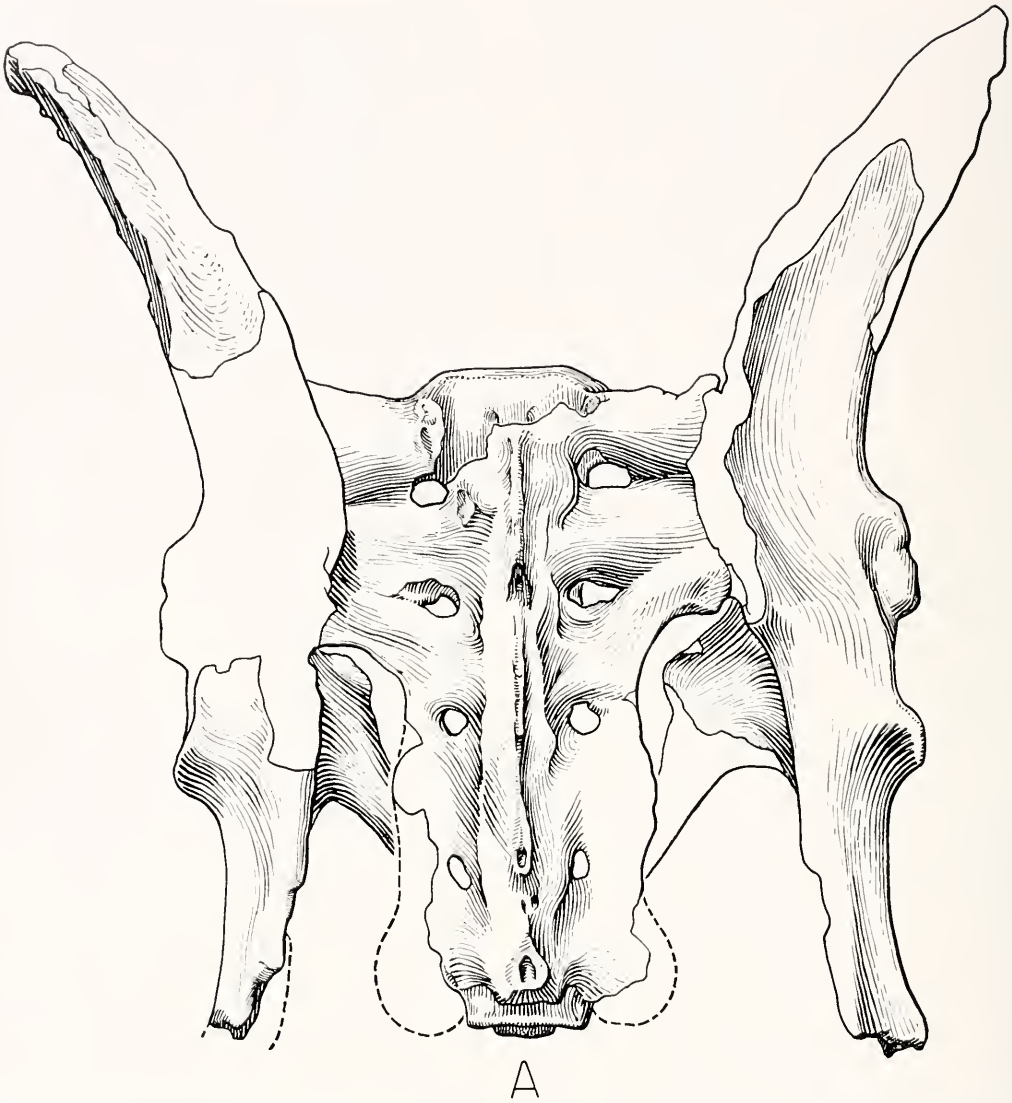
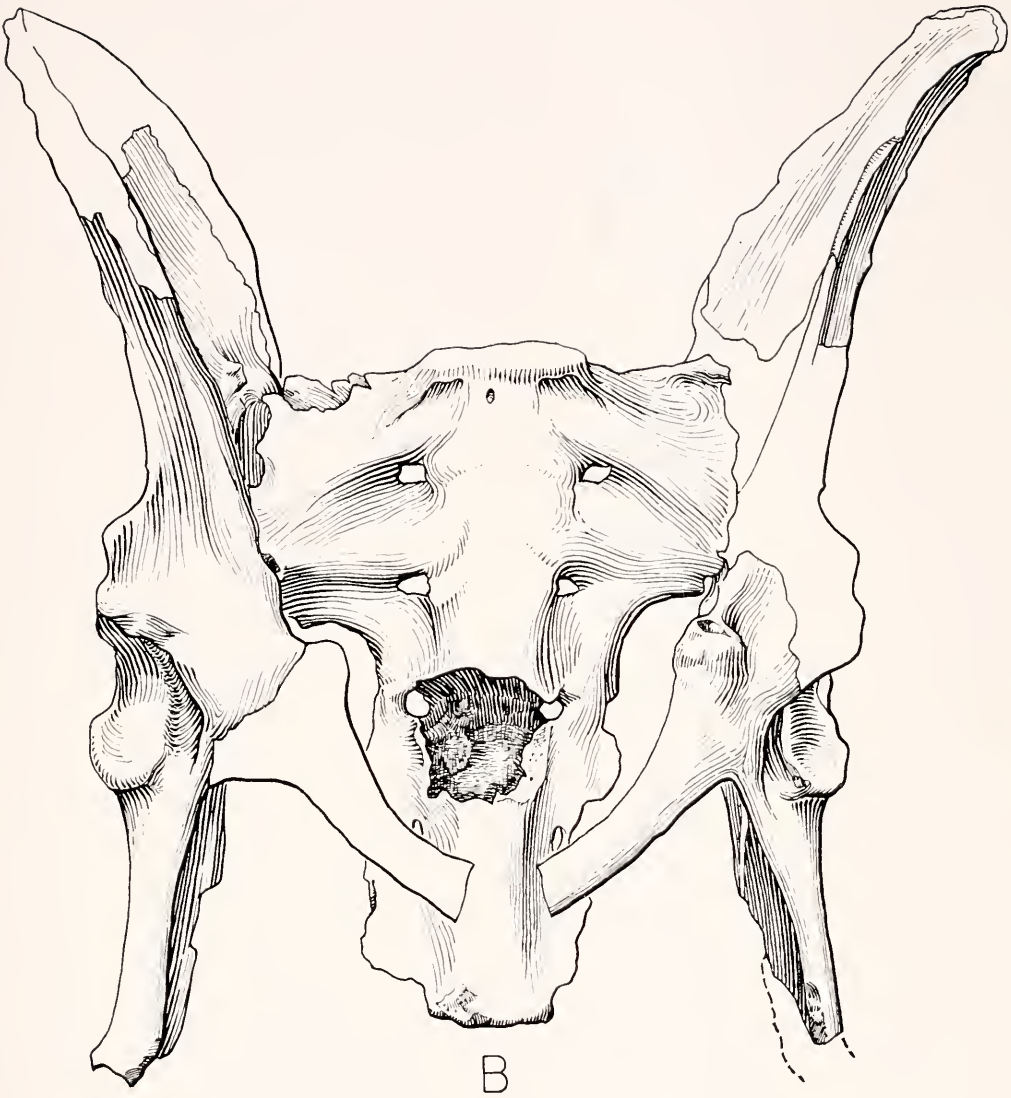


Figure 7. *Leptorycteropus guilielmi* gen. et sp. nov. Dorsal (A), and ventral (B), views of pelvis and sacrum. × 3/5.

area in the living species, all of it dorsal to the linea glutea superior and marked on the gluteal face by prominent muscle scars,[1] may be another specialization within the *Orycteropus* lineage, one perhaps associated

[1] Precisely what muscles is uncertain. The seeker after usable information on bone-muscle relationships in the monograph of *Orycteropus afer* is usually disappointed. Sonntag (1925, 1926) treated the two systems as though they bore virtually no relation to each other, providing the scantiest of data on the exact areas of origin and insertion on the bones. Of two earlier writers, one (Humphrey, 1869) is vague and the other (Galton, 1869) had no skeleton at hand while he was dissecting.



with the extensive use of the hind leg and tail during digging (p. 218); Broom (1905) saw in it a resemblance to *Diademodon*. The tubercle for M. rectus femoris is about as in *Orycteropus*, less extended, less crest-like than in *Plesiorycteropus*. The acetabulum is similar to that of the living form. The articular area is not as expanded posterodorsally and, on the ventral side, does not extend as far posteriorly. The ischium is very concave on its medial surface, the concavity deepening to a fossa at the level of the acetabulum. The bone does not increase in depth in the part preserved. A small spina ischiadica is present. The part of the pubis preserved is similar in structure and proportions to that of *Orycteropus*, differing in the possession of a sharper crest on the ventral surface and in being directed more ventrally. The obturator fora-

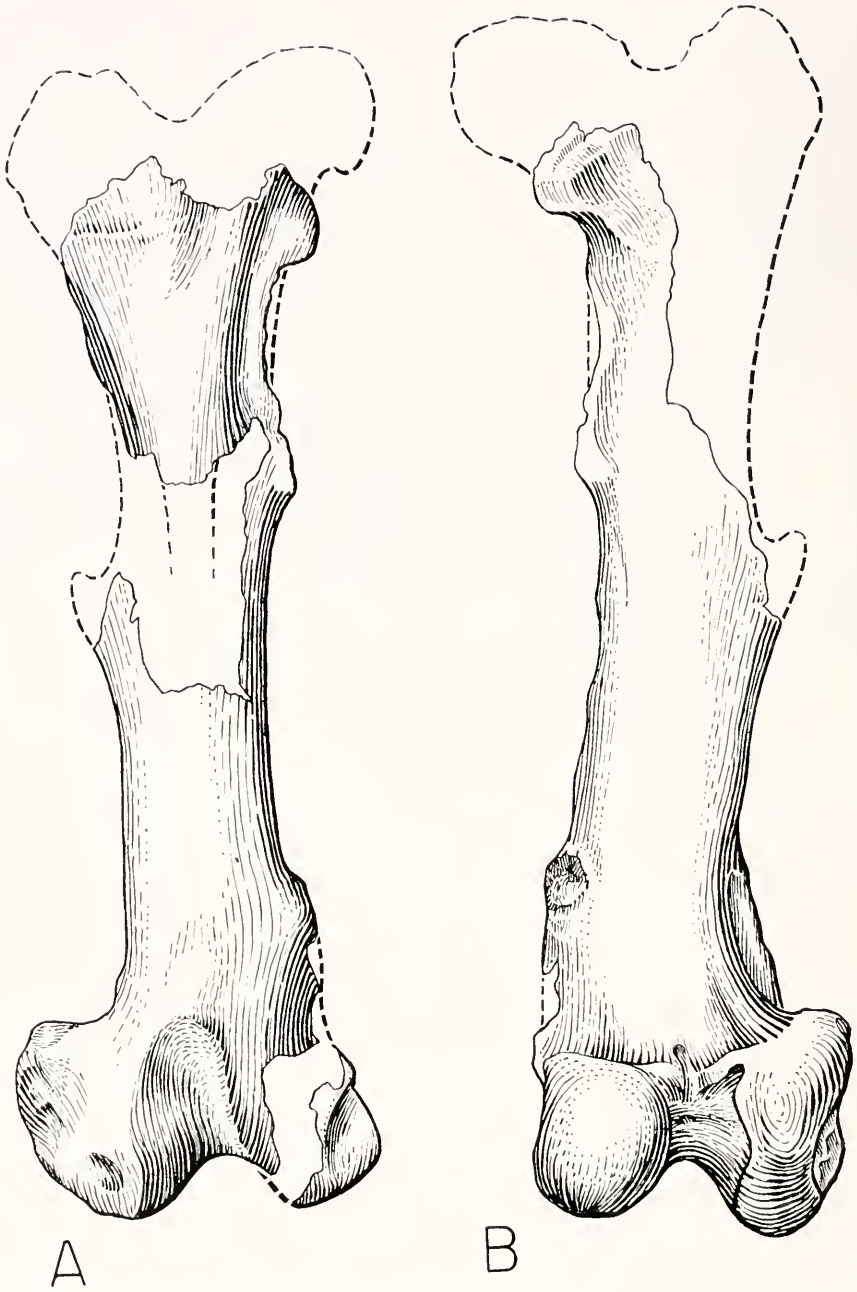


Figure 8. *Leptorycteropus guilielmi* gen. et sp. nov. Anterior (A), and posterior (B), views of right femur. × 3/2.

men, while similar in general outline to that of the living form, is thus relatively larger and deeper, at least anteriorly. The pectineal (iliopectineal) process has the form of a large tubercle and is much less salient than that of *Orycteropus*.

The whole of the proximal end of the femur is missing, together with much of

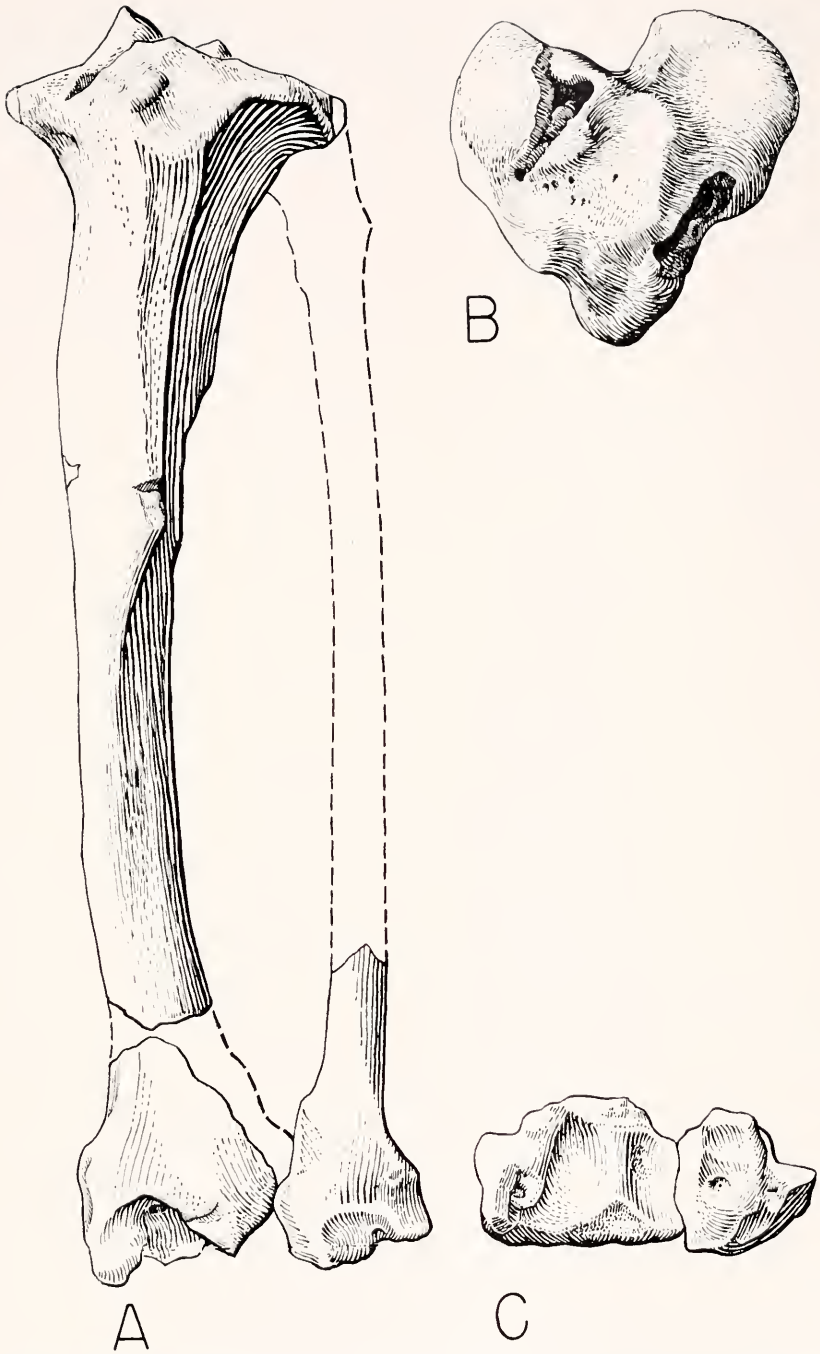


Figure 9. *Leptorycteropus guilielmi* gen. et sp. nov. Anterior (A), proximal (B), and distal (C), views of right tibia and distal end of right fibula. × 3/2.

the anterior face of the shaft. The posterior face is somewhat flattened, as in *Orycteropus*; what is present of the anterior face suggests that it, too, was similar in shape to that of the living form. The lesser trochanter in position, inclination and form is also similar, and is likewise connected by a crest to a pectineal tubercle on the medial side of the bone a little above the level of the third trochanter. Only the base of the latter remains. The distal end is similar in every feature to that of *Orycteropus* except for being relatively more slender in the shaft above the distal articular area. The structure and proportions of the bone as a whole are closer to those of the living form than to *Myorycteropus* and, especially, *Plesiorycteropus.*

The proximal portion of the left tibia and the distal portion of the right fortunately overlap, permitting a good estimate of the length of the bone. Allowing for the missing proximal end of the femur (Fig. 8), the two bones seem about equal in length, with the tibia perhaps slightly longer. The bone is more slenderly constructed than is that of *Orycteropus,* both in the shaft and in the relative width of the proximal end, and is by no means as bowed medially as it is in *O. afer.* The proximal articular areas are essentially similar in the two genera. Tibia and fibula are also fused at their upper ends, although the area of fusion is less massive in *Leptorycteropus.* In agreement with *O. gaudryi,* there is an uninterrupted rim of bone running from the patellar tuberosity to the junction with the fibula, a contrast to the living species in which a deep notch is present in this area. The tuberosity and the cnemial crest are relatively less salient than in *Orycteropus,* the crest terminating slightly higher on the shaft. Distally, the interosseous crest is much less prominent than in *Orycteropus,* otherwise agreement between the two forms is close. The distal end of the fibula differs again in the lesser development of the interosseous crest, and also in the relatively smaller lateral malleolus. As in the case of the femur, the tibia and fibula of *Leptorycteropus* are closer to those of the living form than to those of *Myorycteropus* and *Plesiorycteropus.*

Measurements in mm.

Dentition

	C	$P^{\underline{1}}$	$M^{\underline{2}}$	$M^{\underline{3}}$	$P_{\overline{1}}$	$P_{\overline{2}}$	$P_{\overline{3}}$	$P_{\overline{4}}$
Length	5.9	3.5	11.1	7.4	3.6	5.1	4.8	4.9
Width	3.1	1.6	7.0	6.9	1.6	1.8	1.8	2.7

Skull

Width across canines	20.8
Width of cranial roof across post-orbital processes	49.6
Depth of ramus beneath P_2, medial side	10.4

Vertebrae

C. 3, length of centrum	7.7
length of zygapophyses	13.1
C. 4, length of zygapophyses	12.4
C. 6, length of centrum	8.2
width of anterior face of centrum	12.5
height of anterior face of centrum at center	4.7
C. 7, length of centrum	8.3
D. 6(?), length of centrum	9.4
width across postzygapophyses	10.6
Width of anterior face of centrum[1]	11.9
height of anterior face of centrum at center	5.0
width of posterior face of centrum[1]	12.8
height of posterior face of centrum at center	5.5
D. 11, length of centrum	10.7
length at zygapophyses	15.1
width across postzygapophyses	12.4
width of anterior face of centrum[1]	13.6
height of anterior face of centrum at center	5.1
width of posterior face of centrum[1]	15.3
height of posterior face of centrum at center	5.8
D. 12, length of centrum	11.3

[1] Excluding the rib facets.

length at zygapophyses	17.3
width across prezygapophyses	12.5
width across postzygapophyses	10.3
width of anterior face of centrum[1]	14.0
height of anterior face of centrum at center	5.4
width of posterior face of centrum[1]	15.4
height of posterior face of centrum at center	6.5
D. 13, length of centrum	12.3
length at zygapophyses	17.7
width across prezygapophyses	11.8
width across postzygapophyses	10.2
width of anterior face of centrum[1]	15.5
height of anterior face of centrum at center	6.1
width of posterior face of centrum[1]	16.8
height of posterior face of centrum at center	6.7
L. 3, length of centrum	13.8
width across prezygapophyses	13.5
width of anterior face of centrum	14.9
height of anterior face of centrum at center	6.6
width of posterior face of centrum	16.1
height of posterior face of centrum at center	7.4
L. 4, length of centrum	14.0
width of anterior face of centrum	14.4
height of anterior face of centrum at center	7.1
width of posterior face of centrum	16.3
height of posterior face of centrum at center	7.8
L. 5, length of centrum	14.0
length at zygapophyses	20.2
width across prezygapophyses	14.2
width across postzygapophyses	13.0
width of anterior face of centrum	14.6
height of anterior face of centrum at center	7.0
width of posterior face of centrum	15.7
height of posterior face of centrum at center	7.5
L. 6, length of centrum	13.4
length at zygapophyses	19.9
width across prezygapophyses	14.0
width across postzygapophyses	13.3
width of anterior face of centrum	14.1
height of anterior face of centrum at center	6.8
width of posterior face of centrum	16.4
height of posterior face of centrum at center	7.4
L. 7, length of centrum	14.7
length at zygapophyses	21.7
width across postzygapophyses	16.5
width of anterior face of centrum	15.3
height of anterior face of centrum at center	6.8
width of posterior face of centrum	18.1
L. 8, length of centrum	13.8
length at zygapophyses	22.0
width across prezygapophyses	17.2
width across postzygapophyses	18.4
width of anterior face of centrum	18.6
width of posterior face of centrum	19.7
height of posterior face of centrum at center	7.0
Sacrum, length of centra	71.1
width across iliac articulations	53.5
length of iliac articulation	26.8
height of iliac articulation	13.8
width at junction of S. 3 and 4	26.4
width of centrum of S. 1	18.5
height of centrum of S. 1 at center	6.9
width of centrum of S. 5	13.7
height of centrum of S. 5 at center	6.8
Cd. 1, length of centrum	15.5
length at zygapophyses	21.9
width across prezygapophyses	10.8
width across postzygapophyses	9.0
width of anterior face of centrum	13.5
height of anterior face of centrum at center	6.6
width of posterior face of centrum	13.2
height of posterior face of centrum at center	7.1
Cd. 3, length of centrum	17.1
width of anterior face of centrum	12.7
height of anterior face of centrum	8.3
width of posterior face of centrum	13.7
height of posterior face of centrum	8.3
Cd. 6, length of centrum	19.2
width of anterior face of centrum	12.0
height of anterior face of centrum	9.1

width of posterior face of centrum	12.4
height of posterior face of centrum	9.3
Cd. 7, length of centrum	20.2
width of anterior face of centrum	11.2
height of anterior face of centrum	9.2
width of posterior face of centrum	11.9
height of posterior face of centrum	9.5

Ratios of height to width [100h/w] in the centra of presacral vertebrae

	Leptorycteropus	*Orycteropus*
C.6 ant.	37.6	41.4
D.6(?)		
ant.	42.0	51.2
post.	43.0	50.9
D.11		
ant.	37.5	50.8
post.	37.9	41.2
D.12		
ant.	38.6	47.2
post.	42.2	35.5[2]
D.13		
ant.	39.4	37.8[2]
post.	40.0	38.7
L.3		
ant.	44.3	50.0
post.	44.6	49.3
L.4		
ant.	49.3	51.0
post.	47.9	48.3
L.5		
ant.	47.9	50.5
post.	47.8	48.9
L.6		
ant.	48.2	51.4
post.	45.1	48.0
L.7 ant.	44.4	47.2
L.8 post.	36.1	39.0

Anterior extremity

Humerus, anteroposterior diameter near center of shaft	10.0
transverse diameter near center of shaft	8.9
transverse diameter of distal end	27.5
anteroposterior diameter of distal end	11.7
anteroposterior diameter of trochlea	10.6
transverse diameter of trochlea	16.3
proximodistal diameter near entepicondyle	15.4
Radius, anteroposterior diameter near center of shaft	8.3
transverse diameter near center of shaft	5.6
transverse diameter of distal end	16.5
anteroposterior diameter of distal end	10.9
Ulna, anteroposterior diameter near center of shaft	11.1
transverse diameter near center of shaft	5.5
Mc. II, transverse diameter of distal end	7.9
anteroposterior diameter of distal end	7.0

Posterior extremity

Pelvis, preacetabular length of ilium (est.)	65.0
width of ilium at center	12.3
anteroposterior diameter of acetabulum	17.8
dorsoventral diameter of acetabulum	15.9
width at M. rectus femoris tubercle	16.4
width of ischium anterior to spina ischiadica	7.0
depth of ischium anterior to spina ischiadica	13.2
depth of descending portion of pubis	5.6
width of descending portion of pubis	6.8
Femur, transverse diameter of shaft below third trochanter	15.4
transverse diameter of distal end	28.3
anteroposterior diameter of distal end	27.4
Tibia, length (est.)	111.0

[2] The medial parts of the rib facets in posterior dorsals have become incorporated into the articular surfaces of the centra, thus increasing their widths.

anteroposterior diameter of proximal end	29.5
transverse diameter of proximal end	30.3
anteroposterior diameter at center of shaft	14.8
transverse diameter at center of shaft	8.8
anteroposterior diameter of distal end	13.3
transverse diameter of distal end	19.5
Fibula, anteroposterior diameter of distal end	12.2
transverse diameter of distal end	12.7

CONSPECTUS OF THE FOSSIL ORYCTEROPODIDAE

Leptorycteropus

As evident from the description, *L. guilielmi* is the most generalized member of the family so far known. Although definitely oryeteropodid—and orycteropodine—in structure it is, despite its comparatively recent age, primitive in various features, such as a short facial region, a relatively large canine (and perhaps a complete dentition), a mandibular symphysis extending back to a point beneath the anterior cheek teeth, relatively slender limb bones (Figs. 10, 12–13), humerus without a well defined deltopectoral area, tibia with a relatively weak enemial crest, and so on.

Until now the Tubulidentata have perforce had to be considered in the light of *Orycteropus*, a rather specialized form. *Leptorycteropus* provides a better vantage point from which to assess phylogeny, relationships and adaptations within the order.

Orycteropus. (Figures 10–13)

I follow those (e.g., Allen, 1939: 270–272) who include all living forms in *O. afer*. Confined today to subsaharan Africa the species evidently enjoyed a more northerly distribution within the continent in relatively recent times, to judge from a partial skull found in the Tanezrouft region, central Sahara, in deposits of very late Pleistocene or early Recent age (Romer, 1938: 177).

A number of extinct forms have been referred to the genus. Those so identified only on the basis of isolated teeth or of maxillary and mandibular fragments must be regarded with reserve. *Leptorycteropus*, for the molars, and *Myorycteropus*, for the cheek teeth as a whole, show that oryeteropodines differing decidedly from *Orycteropus* in cranial and postcranial characters may have teeth so similar to those of *Orycteropus* as to make generic discrimination on such evidence impossible.

The following, arranged in geochronologic order, may on available data be included in the genus:

O. mauritanicus Arambourg (1954: 295; 296, as *O. gaudryi*; 1959: 42–53) from the "Vindobonian" of Algeria is known from much of a badly crushed skull, mandibular fragments, tibia and elements of the fore and hind feet. Larger than *O. gaudryi*, it is, next to that form, the best known extinct member of the genus. Five antemolar teeth are present, the maxillaries extending beyond them anteriorly for an unknown distance; the tooth rows are more arched and more convergent anteriorly than in the other species, the premolars are somewhat larger, and M^{1} is longer than M^{2}. The facial region would appear to have been longer relative to the cranial than in *O. gaudryi*. The tibia resembles that of *O. gaudryi* in slenderness and lesser degree of bowing; that of *O. afer* in the structure of the proximal end. The rather narrow astragalus has a relatively longer neck than that of any other orycteropodid in which this bone is known. Mt. V, as in *O. gaudryi*, is relatively longer than in *O. afer*.

O. gaudryi Major (Colbert, 1941) is by far the best known of any of the extinct orycteropodids; nearly all parts of the postcranial skeleton except the clavicle and pelvis are present in an individual from Samos. This and other specimens from that locality have been admirably described and compared with *O. afer* by Colbert, and de

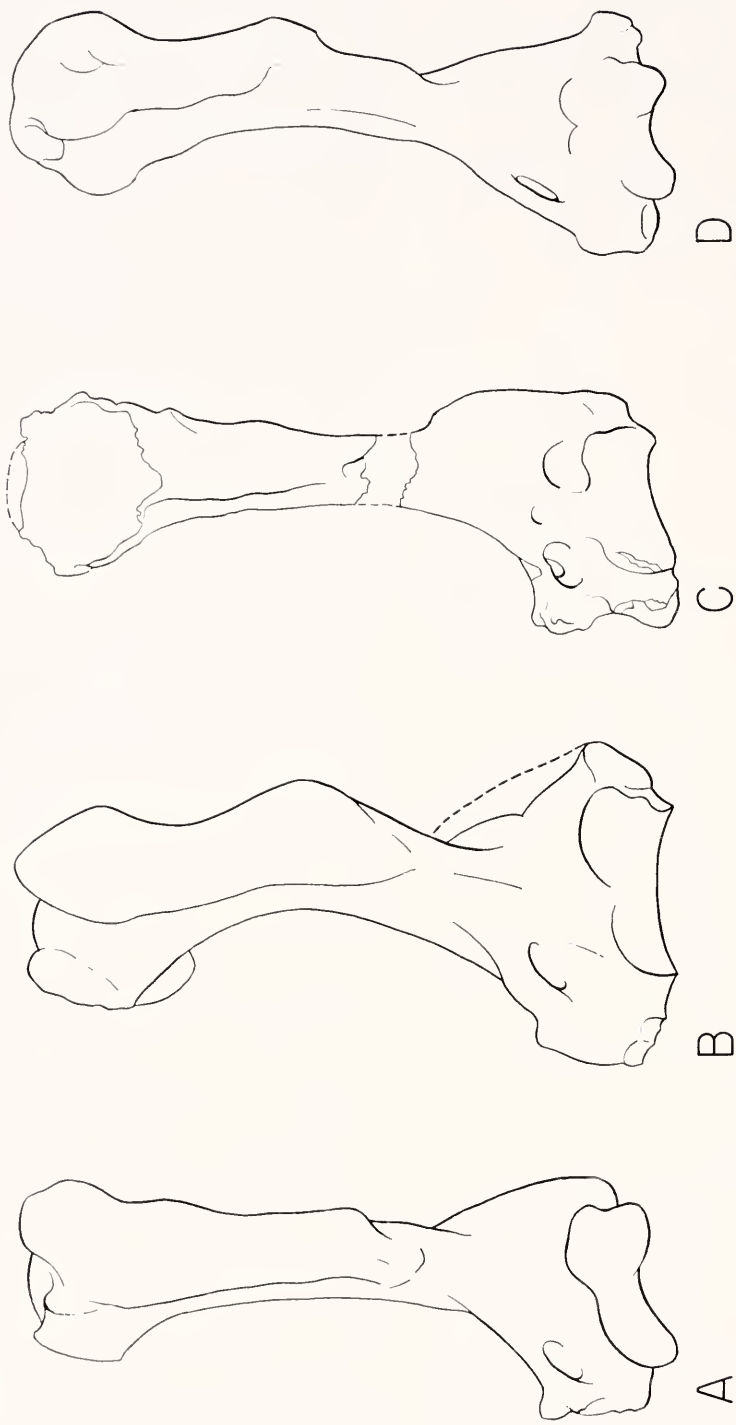


Figure 10. Anterior views of left humeri of *Orycteropus* (A), *Myorycteropus* (B), *Leptorycteropus* (C), and *Plesiorycteropus* (D). This and the three following figures are not to scale; *O. afer* is approximately twice the size of the others. *Orycteropus* and *Myorycteropus* are after MacInnes (13B modified); *Plesiorycteropus* is from Lamberton (10D, 12D and 13D reversed).

Beaumont (1970) has contributed supplementary observations. In addition to the Samos quarries, the species has long been known to occur at Maragha in Iran and has also been recorded from the Ukraine. *O. gaudryi* is the smallest of the several species so far described that can be referred with assurance to the genus. The molars are larger relative to the size of the skull than in the living species. A complete set of premolars is usually present, but no tooth anterior to them is known. The rostrum extends well beyond P^1, but is more tapering and the palate narrower than in *O. afer*. The nasals are more deeply inset between the frontals, the occiput is more nearly vertical and narrower relative to height, the facial region is shorter, the olfactory area is less expanded, the anterior border of the orbit lies over the anterior part of M^2, and the ascending ramus is more vertically inclined. The skull is longer relative to the leg bones than in *O. afer*. The posteranial skeleton is in general more slenderly constructed as the bones, both axial and appendicular, are relatively narrower. The manus, but not the pes, is relatively smaller than in the living species. Mc. V and the fifth digit of the pes are relatively longer, and the great trochanter of the femur is lower relative to the head than in *O. afer*. A further difference, not mentioned by Colbert but evident from his figures and measurements, lies in the proportions of the hind leg bones—the tibia of *O. gaudryi* is definitely longer than the femur, whereas the reverse is the case in other orycteropodids with the possible exception of *Leptorycteropus*.

O. depereti Helbing (1933), known from a nearly complete skull from the Pliocene of Perpignan, southern France, is comparable in size to *O. mauritanicus* and, as in that species, has five antemolar teeth, with the maxillary extending beyond them anteriorly for an unknown distance. While agreeing with *O. gaudryi* in rostral width and in the possession of a nearly vertical occiput, the species approaches *O. afer* in the width of the palate relative to the total width of the facial region, the rather more inflated olfactory area, the lesser degree of convergence of the tooth rows anteriorly, the position of the anterior border of the orbit above the posterior border of M^2, and the greater width relative to height of the occiput.

O. pottieri Ozansoy (1965: 45–46) from the late Pliocene, Astian, of Turkey is based on a mandibular ramus that lacks the symphysis.[1] Five antemolar teeth are present, as in *O. mauritanicus* and *O. depereti*. The condyle is not as high relative to the alveolar level as in *O. gaudryi* and *O. afer*; the inclination of the ascending ramus is comparable to that in the living species. Ozansoy gave no measurements. To judge from his figures, the length of the lower tooth row of *O. pottieri* may have been greater than that of the upper tooth row of *O. depereti*: ca. 76.0 mm as against 64.0 mm. Differences of this magnitude, however, occur in *O. afer*, and in individuals of that species, e.g., M.C.Z. 2097, the lower tooth row may be longer than the upper. The possibility, even probability, exists that *O. pottieri* is based on a jaw of the essentially contemporaneous *O. depereti*. It is unfortunate that no information on the limb bones is available as it would be interesting to learn if these were advanced in the direction of *O. afer* over those of *O. gaudryi* and *O. mauritanicus*.

O. sp. (*O.* sp. cf. *O. aethiopicus* Sundevall, Dietrich, 1942: 54). Three specimens, a ramus fragment with $M_{\overline{3}}$ and two Mc. V, all isolated finds, have been collected in the Laetolil area, Tanzania. Whether they were found in the Pliocene or the

[1] A maxillary and some isolated teeth and limb bones were mentioned but not described. Ozansoy did not designate a type, nor give numbers to his specimens, nor state the institutions in which they are preserved. The mandible, as the only bone described, is obviously the type. Presumably, most if not all, of his specimens are in the collections of the Institut d'études et de recherches minières de Turquie (M.T.A.), Ankara.

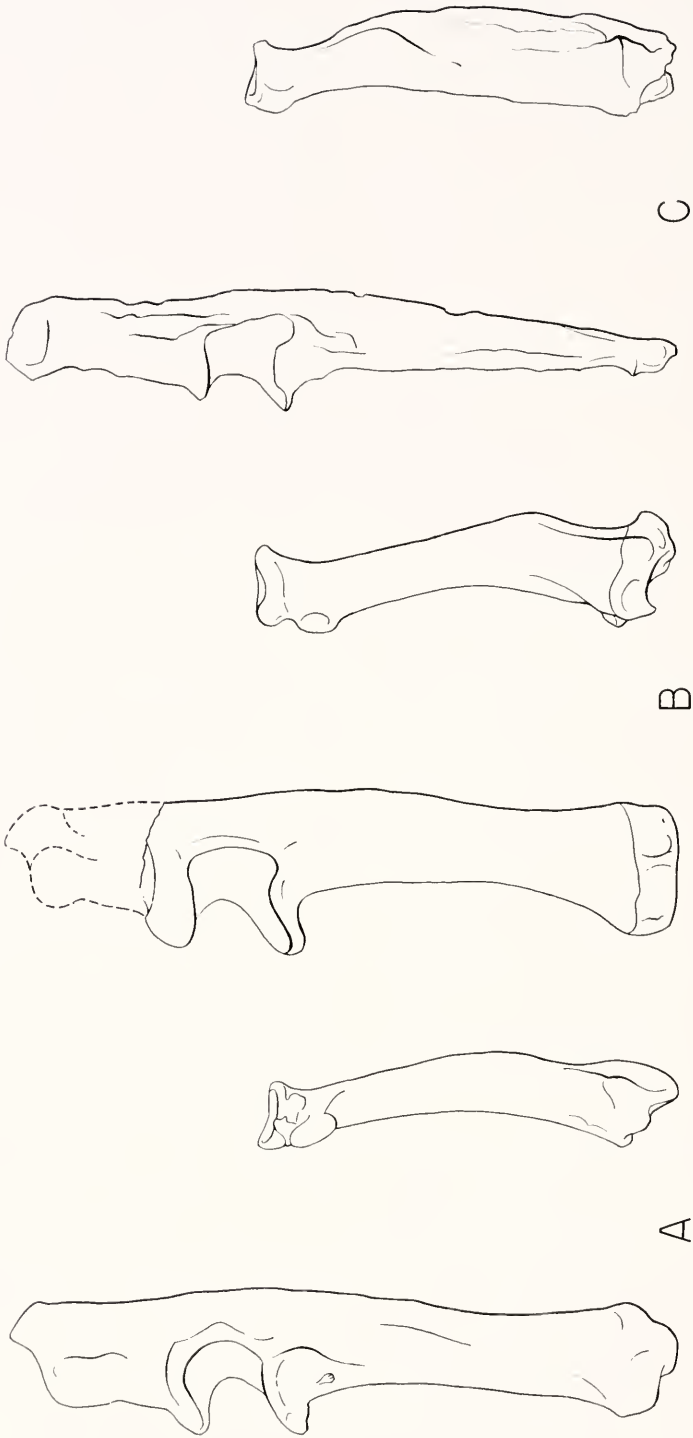


Figure 11. Lateral views of left ulnae and medial views of left radii of *Orycteropus* (A), *Myorycteropus* (B), and *Plesiorycteropus* (C).

early Pleistocene deposits there (Maglio, 1969: 12), or in both, is not known. The metacarpals are essentially identical with those of *O. afer*, but, as Leakey (1967: 19) has pointed out, this form could pertain to *O. crassidens* or, it may be added, to some species as yet unknown.

O. crassidens MacInnes (1956: 28–37) from the later Pleistocene of Kenya, type from Rusinga Island (found in deposits of uncertain age but suspected by MacInnes to be not earlier than late middle Pleistocene and possibly younger), referred specimen from Kanjera, is known from a partial skull, a nearly complete mandible and elements of the axial and appendicular skeleton. Not surprisingly, this form is very close to the living species, differing in only a few characters, such as relatively larger teeth and more vertically implanted M^3. It may prove to be no more than subspecifically distinct. MacInnes (p. 35) tentatively assigned to it an isolated ungual from Rusinga. This bone differs from the unguals of *O. afer* and of the Kanjera specimen of *O. crassidens* in characters that suggest less proficiency in digging. It may not be referable to the genus, and is indeed the sort of ungual one would expect in *Leptorycteropus*.

The following should, I believe, be queried until better known:

O.? sp. (MacInnes, 1956: 27–28), represented by a single molar, identified as M^1, from the early Miocene of Koru, Kenya. The tooth is comparable in size and structure to M^1 of *O. afer*, but this does not necessarily reveal much about the animal that bore it. The upper molars of *Leptorycteropus* (p. 187) are also similar in both respects to those of the living species.

O.? sp. (Gabuniya, 1956). This earliest record to date of a tubulidentate in Eurasia consists of part of a left mandibular ramus from the middle Miocene of the Kuban region, North Caucasus. Alveoli of six antemolar teeth and of M_1 are preserved, and also part of the alveolus of M_2. From the high number of antemolars Gabuniya believed the specimen to be a young individual; the marked posterior increase in the depth of the ramus also suggests this. The animal seems to have resembled *Orycteropus* and *Myorycteropus* in the elongation of the muzzle beyond the cheek teeth. It is hoped that additional material sufficient to determine its affinities with greater precision will soon be found.

O.? *browni* Colbert (1933: 2–6) was founded on a maxillary fragment with M^{2-3} from the Nagri of Pakistan. Colbert believed the type to represent an adult individual with molars three-fifths as large as those of *O. gaudryi*. Accepting this, all that can at present be said is that in *O.*? *browni* we have an orycteropodine with M^{2-3} smaller than those known in any described member of the family except *Myorycteropus africanus*.

O.? *pilgrimi* Colbert (1933: 6–7) was described on the basis of an isolated tooth, identified as $M_{\overline{2}}^1$, comparable in size that of *O. gaudryi* from "the lower part of the Middle Siwaliks," which suggests Nagri age. Lewis (1938) referred a specimen from the Dhok Pathan to the species; this consists of an incomplete cranium, including the posterior portion of the palate with molars, and part of the ascending ramus. The cranium, as restored by him, and the molars agree in general with *Orycteropus* but nothing is known of the facial region.

O.? sp. (*O.* sp. cf. *O. afer* Pallas, Kitching, 1963). Two specimens, an isolated M^1 and a ramus fragment with M_3 and broken M_2, have been recovered from the Makapan breccias. Kitching's measurements indicate a form with lower molars that are slightly longer but notably narrower proportionaly than those of the type of *O. crassidens*.

Myorycteropus
Figures 10–13

M. africanus MacInnes (1956) from the early Miocene of Rusinga and Mfwanganu

[1] Lewis (1938: 403) regarded it, incorrectly I think, as M^2. Colbert in the caption to his figure 5, states "... anterior edge of tooth facing the left": "left" appears to be a *lapsus* for "right".

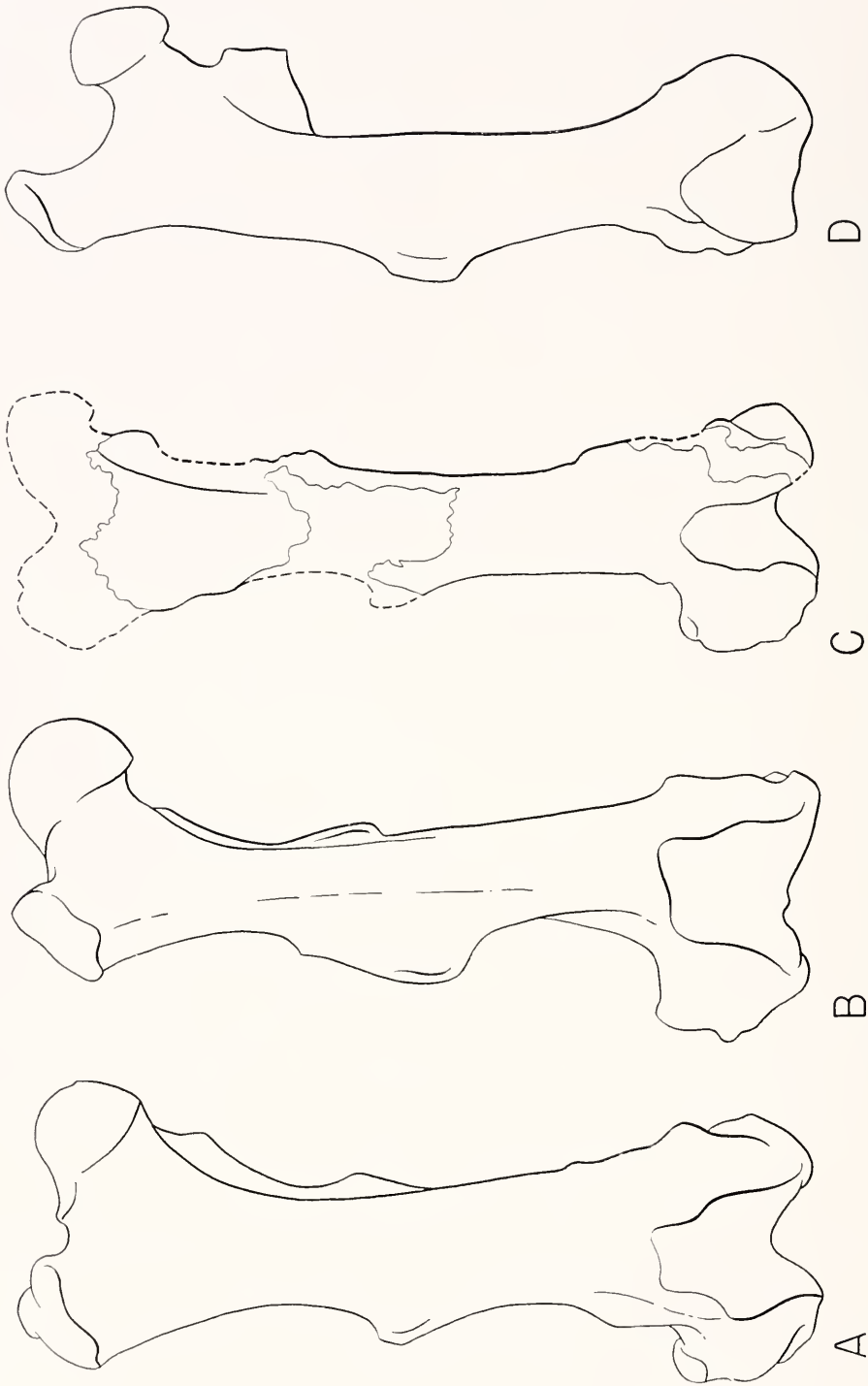


Figure 12. Anterior views of right femora of *Orycteropus* (A), *Myorycteropus* (B), *Leptorycteropus* (C), and *Plesiorycteropus* (D).

Islands, Kenya, the only species, is the earliest adequately known member of the order and also the most specialized of described orycteropodines. The type consists of an incomplete maxilla with P^3–M^3, some isolated teeth, a ramus with $P_{\overline{1}}$–$M_{\overline{3}}$ but lacking the symphysis, coronoid process and part of the angle, elements of the vertebral column and a rather good representation of the appendicular skeleton. A complete series of premolars was present and a very small tooth found in the matrix surrounding the type is perhaps a fifth upper antemolar. As in *O. mauritanicus*, M^1 is longer than M^2. By itself the dentition would not suffice to exclude the species from *Orycteropus*, but it is quite otherwise with respect to the skeleton. As MacInnes noted, the skull appears to have been relatively lower than that of *Orycteropus*, the ascending ramus of the mandible meets the horizontal at a much shallower angle, and the condyle evidently extended posterad of the angular process. The symphysis is lacking. Since there is no indication of it on the part preserved, which extends forward to $P_{\overline{1}}$,[1] it would appear that the muzzle was prolonged anteriorly beyond the teeth, in contrast to *Leptorycteropus* and in general agreement with *Orycteropus*. Mandible and molars are somewhat larger relative to leg bone lengths than in *O. afer*. The distal portion of the scapular spine has an expansion on the prespinous side opposite the metacromion. The clavicle is larger, relatively, than in *Orycteropus*. The humerus is laterally more bowed, the deltoid area relatively larger, and the distal end relatively much wider than in *Orycteropus*. Radius and ulna of *Myorycteropus* are also relatively wider distally. The radius is somewhat shorter relative to the humerus than in the other forms, and differs from that of *Orycteropus* in the humeral and proximal ulnar articulations. The metacarpals and phalanges of the forefoot are relatively larger than in *O. afer*; Mc. V in both is equally short relative to Mc. II, but in *O. gaudryi* Mc. V is relatively longer. The trapezium covers a much larger part of Mc. II than is the case in *Orycteropus*. The unguals are relatively narrower than in *Orycteropus* and have longer plantar protuberances. The pelvis is more slenderly constructed. The femur, in contrast to those of *Orycteropus* and—so far as known—*Leptorycteropus*, has a more slender shaft, especially proximally, a more globular head set on a more distinct neck and separated from the great trochanter by a deeper notch, and a much larger third trochanter. The shaft of the tibia is more compressed transversely and the cnemial crest terminates in a blunt tubercle. MacInnes restored the proximal end of the bone as having the articular area for the femur decidedly oblique to the long axis, with the lateral condyle facing more outward than upward (1956, fig. 9, (b) 1, p. 20). Attempts at a paper fit of the tibia, thus restored, to the femur result in an outward inclination of the former bone at an angle of about 45° to the long axis of the latter, surely an impossible position. MacInnes stated that the tibia was somewhat crushed and preserved no point of contact with the fibula, which lacked the proximal epiphysis. As his restoration made no allowance for this missing portion I present (Fig. 13B) an alternative one that does and in so doing provides a better fit with the femur. There are various differences between the tarsi of the Miocene and living forms, the most conspicuous of which lie in the astragalus: in *Myorycteropus* the medial flange of the trochlea does not extend distally on the neck, and both neck and head are wider transversely and flatter dorsoventrally. The pes, like the manus, was relatively larger than in *Orycteropus*.

Lavocat (1958: 142) has commented regarding the distinctive characters of *Myorycteropus*: "On voudrait être assuré

[1] The lighting of MacInnes' figure 4, plate 1 is such as to suggest that the symphysis began beneath P_{1-2}. Examination of the specimen, however, reveals no trace of it.

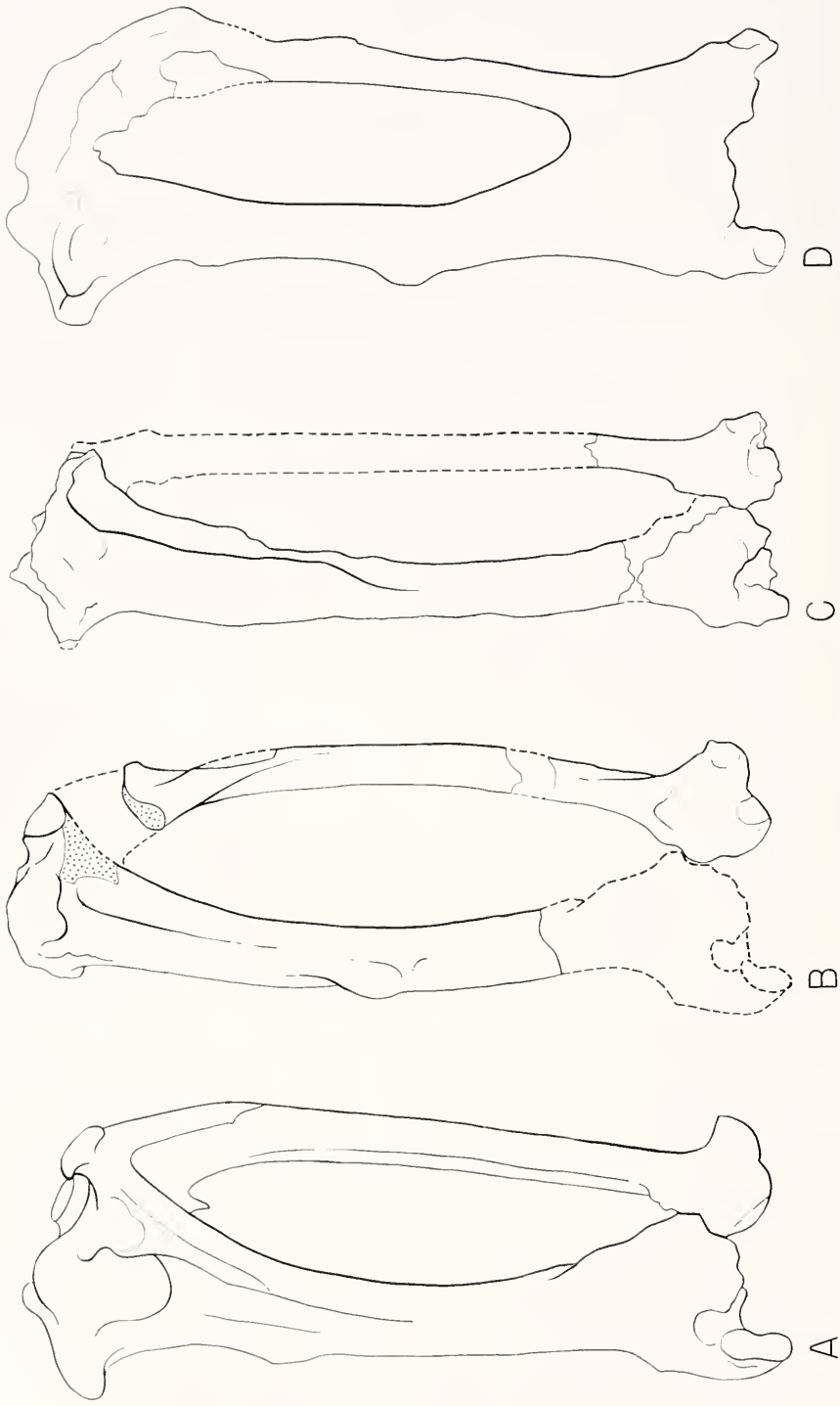


Figure 13. Anterior views of left tibiae-fibulae of *Orycteropus* (A), *Myorycteropus* (B), *Leptorycteropus* (C), and *Plesiorycteropus* (D).

qu'elles nécessitent réellement l'admission d'un nouveau genre." I believe, on the contrary, that one could hardly ask for better generic characterization than is afforded by the postcranial skeleton.

Plesiorycteropus
Figures 10–15

The most isolated tubulidentate, morphologically as well as geographically, is *P. madagascariensis* Filhol 1895. This is an extinct Recent species known from several of the superficial deposits of the island—Ampasambazimba, Ambolisatra, Antsirabe, Belo-sur-Mer, Beloha, and Tsiravé. For one of these, Ampasambazimba, a C^{14} date of 1035 ± 50 B.P. has been obtained (Tattersall, 1973B).

The type is the cranial portion of a skull. Filhol's description of it was exceedingly brief, expressed some doubt as to affinities and was unaccompanied by figures. *P. madagascariensis* remained virtually a *nomen dubium* for half a century.[1] Real knowledge of it dates from Lamberton (1946), who redescribed the type (which he did not specifically identify, but which is obviously M.N.H.N. no. 1906–717, the specimen shown in his plate 1, figs. b′ and b″) and referred a number of additional specimens to the species. These were: two crania, one with the nasals attached, a sacrum, more than sixteen other vertebrae, all of them incomplete, two humeri, a radius, an ulna, several metacarpals and phalanges, much of a pelvis, eight femora (from his text it would seem that Lamberton had at his disposal pelves and femora other than those he described or listed, but he did not state how many), three tibiae-fibulae, and three astragali. I have been able to study a cranium evidently not seen by him and some postcranial elements that he may or may not have seen, a point which cannot be determined from his paper. Some of these bones are strikingly different from the corresponding elements of the other orycteropodids, which resemble each other in most of their known parts much more than any one of them does *Plesiorycteropus*. Lamberton noted resemblances in the Malagasy form not only to *Orycteropus* but also to dasypodids, myrmecophagids and manids. *Plesiorycteropus* merits extended discussion.

Two questions at once present themselves—How good is the evidence that the various skeletal elements referred to *P. madagascariensis* really pertain to one form?, and What weight should be given to the resemblances to this group or to that?

As regards the first question, Lamberton himself seems to have had lingering doubts (1946: 47, 49) since he expressed concern that some of the bones might, after all, represent manids and dasypodids. Lavocat (1958: 139) echoed his uncertainty. I do not believe that there is any real justification for such hesitation. None of the bones in question, with the very dubious exception of the femur (see below), could be referred to any of the other groups known to inhabit or to have inhabited the island. They therefore pertain to one or to several animals that represent an additional group or groups. If they represent several then it is indeed remarkable that only one kind of peculiar humerus, one kind of peculiar femur, one kind of peculiar tibia-fibula and so on—all of appropriate size to belong together—is known. The

[1] It was not listed by Simpson in his classification (1945)—and for good reason. He plainly stated (p. 34), "An effort has been made to include all genera that are well defined . . . . Nevertheless, a great number . . . . surely or probably invalid . . . . . or . . . so poorly known as now to have little real meaning are deliberately omitted." Late in 1942, when the manuscript of the classification was closed (p. 1x), *Plesiorycteropus* amply fulfilled the last of these criteria for exclusion. I call attention to all this only because statements occur in the literature, sometimes with apparent surprise, sometimes with overtones of chortling, that this or that obscure genus "is not in Simpson" or that some revision made before publication but after the closing of the manuscript, when he was on active service in the army, was "overlooked" by him.

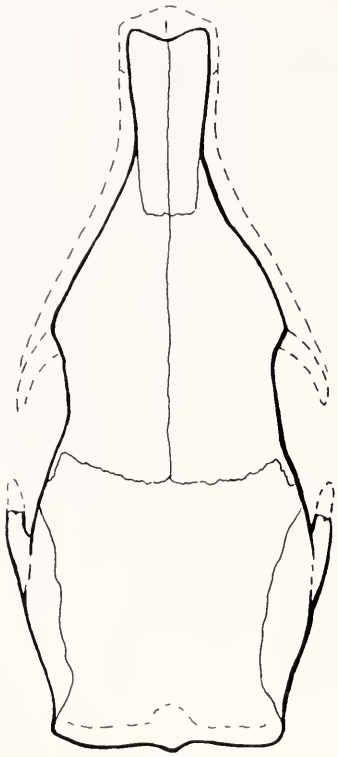


Figure 14. *Plesiorycteropus madagascariensis*. Tentative reconstruction of the skull in dorsal view. Based on the type and an unnumbered specimen in the Muséum Nationale d'Histoire Naturelle, and on Lamberton, 1946: pl. 1, fig. c. × 1/1 approx.

bones have been found in various combinations at several localities. For example, at Ambolisatra the sacrum was found in articulation with the pelvis, and nine other vertebrae and a cranium were in close proximity; at Tsiravé metacarpals and unguals, five femora, a tibia-fibula and two astragali were collected. The peculiar femur articulates well with the pelvis, the peculiar tibia-fibula with the femur, the peculiar astragalus with the tibia-fibula, etc. It seems evident that we are dealing with the remains of one form only.

Concerning the second question, Lamberton himself came to no positive conclusion as to the affinities of *Plesiorycteropus*. It might be, he thought, a "synthetic type," combining characters of edentates, pangolins and aardvarks. His text gives the impression that he favored the concept of an inclusive Edentata, in the 19th century sense of the term, and regarded the fossil as lending some support, as a possible survivor of the ancestral stock, to this now abandoned grouping. But his prose is somewhat elusive on the point. The similarities to dasypodids that he noted are several and striking, but are habitus resemblances (they are discussed below under Adaptation, p. 224), those to myrmecophagids few and minor. It may safely be concluded, with Lavocat (1958: 142), that similarities between *Plesiorycteropus* and edentates are due to convergence. There is no evidence that any member of the Edentata, in the modern taxonomic sense, ever inhabited Madagascar.[1] The similarities to pangolins may be considered together with the more fundamental and more numerous resemblances to orycteropodines.

Skull. Of the facial region only the nasals are known. These are short, suggesting that the face was probably not as long as the cranium. Rather narrow and well inset between the frontals, they widen anteriorly—the reverse of the situation in *Orycteropus*—and their anterior border is concave rather than projecting forward in the midline. The orbital rim is not well defined dorsally and a postorbital process is lacking. The extent of the frontolachrymal suture suggests the presence of a lachrymal that was probably comparable in position and relative size to that of *O.*

[1] That they may have done so was a minor myth of Paleontology that never achieved much currency. It rested on *Plesiorycteropus* (the distal end of a tibia-fibula was figured by Carleton, 1936, as an "unknown type resembling armadillo"), and on limb bones once thought to indicate the presence of a possible relative of the tree sloths (*Bradytherium madagascariensis* Grandidier 1901) but now regarded as probably pertaining to the extinct lemuroid *Palaeopropithecus* (Lamberton, 1947). The degree of convergence between tree sloths and *Palaeopropithecus* in various characters is rather striking.

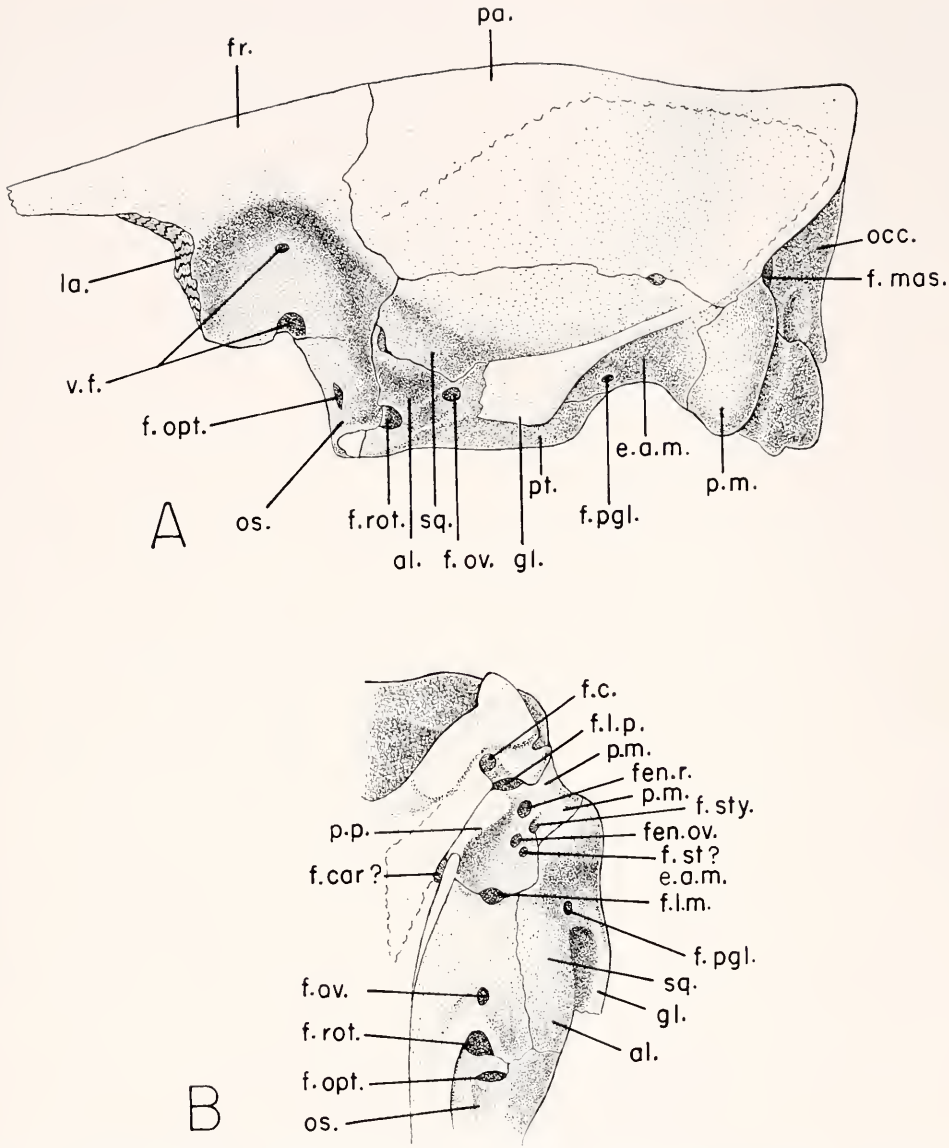


Figure 15. *Plesiorycteropus madagascariensis*. Left lateral, A, and ventral, B, views of cranium. Unnumbered specimen in Muséum Nationale d'Histoire Naturelle. ×3/2.

al., alisphenoid; e.a.m., external auditory meatus; f.c., condylar foramen; f. car?, carotid foramen; f.l.m., foramen lacerum medium; f.l.p., foramen lacerum posterius; f. opt., optic foramen; f. ov., foramen ovale; f. pgl., postglenoid foramen; f. rot., foramen rotundum; f. sty., foramen stylomastoideum primitivum; fen. ov., fenestra ovalis; fen. r., fenestra rotundum; fr. frontal; gl., glenoid process; la., fronto-lachrymal suture; occ., occipital; os., orbitosphenoid; p.m., pars mastoidea; p.p., pars petrosa; pa., parietal; pt., pterygoid; sq., squamosal; v.f., vascular foramina.

gaudryi. This is a contrast to the mandids, in which the lachrymal, when present, is more ventrally situated and has only a small facial portion. The cranial roof is more smoothly rounded across the parietals than in *Orycteropus*, and the area of origin of M. temporalis is poorly developed. The degrees of participation of the frontals, parietals and supraoccipital in the formation of the skull roof are essentially the same as in *Orycteropus*. As in *O. gaudryi*, but not as in *O. afer*, the occiput is essentially vertical. The occipital condyles and foramen magnum are in every respect comparable to those of *Orycteropus*. A lamboidal crest is present, running transversely without the median indentation present in *Orycteropus*. It is confluent laterally with the dorsal margins of the posterior roots of the zygomatic arches. The cranial portion of the squamosal is relatively longer and not as deep as in *Orycteropus*. It meets the frontal and thus excludes the alisphenoid from contact with the parietal. The ascending portion of the orbitosphenoid does not extend as far dorsally as it does in *Orycteropus*.

The position and structure of the glenoid articulation, revealed by the hitherto undescribed specimen in the Muséum Nationale d' Histoire Naturelle, is of great interest. The squamosal sends down a moderately extensive, rather long glenoid projection that is set off below from the side wall of the cranium by a notch. This process bears at its free extremity an elongate, narrow, transversely convex and poorly-defined articular surface for the mandibular condyle.[1] The articulation is thus brought downward to a level corresponding with that of the base of the occipital condyle and below that of the external auditory meatus. This is a point of major contrast to *Orycteropus*, in which the articulation occupies a much higher position—above both condyle and meatus—and of resemblance to manids and other fully myrmecophagous mammals, in which the articulation is on a level with the palate (see p. 220). The glenoid projection differs from that of manids in being relatively smaller, more posteriorly situated and directed more ventrally than anteroventrally. The zygomatic arch was probably reduced, and may perhaps have been incomplete. There is no postglenoid process, as in manids. The postglenoid portion of the skull is longer, relatively, than in *Orycteropus*.

The auditory region is basically orycteropodid, although the auditory meatus is wider and more laterally situated and the epitympanic recess smaller than in *Orycteropus*. There appears to be no epitympanic sinus; one is present in the living form. In both genera the pars mastoidea is large and well exposed on the surface of the skull between squamosal, exoccipital and parietal; it is wider dorsally in *Plesiorycteropus*. In manids there is a large epitympanic sinus and the mastoid exposure is smaller and situated ventrally between squamosal and exoccipital. The foramina of the Malagasy form differ in only a few particulars from those of *Orycteropus*—lachrymal within the orbit rather than on the side of the face, opticum slitlike and aligned dorsoventrally, not round, postglenoid present.

Nothing is known of the mandible or of the dentition. From the lowered position of the glenoid articulation, the loss of the postorbital process, and the evidently weak temporal musculature I would infer that the mandibular rami were reduced to rather straight, slender rods, with little in the way of ascending portions, and that the teeth were greatly reduced if not entirely lost. In other words, the masticatory apparatus of *Plesiorycteropus* resembles that of other fully committed myrmecophagous mammals, which *Orycteropus*, in this respect only, does not (see pp. 226–228).

[1] The projection was lacking in the material available to Lamberton, who identified as the glenoid cavity a shallow depression on the cranium above the foramen ovale. This depression is variably developed in both *Plesiorycteropus* and *Orycteropus*.

The resemblances between *Plesiorycteropus* and the manids in skull structure are adaptive in nature, and hence convergent; those between it and the orycteropodines are indicative of affinity.

Vertebrae. Lamberton did not point out any specific resemblances to manids, and I am unable to detect any. On the other hand similarities to orycteropodines and differences from manids are evident. The centra of the anterior dorsals are much wider than deep, their articular surfaces slightly convex in front and concave behind. The spines of these vertebrae are rather slender, long and inclined posteriorly, not elongate anteroposteriorly, rather than short and upright as in pangolins. The only known posterior dorsal has a slight hypapophysis. The anterior caudals[1] have high, slender spines, the ventral surfaces of the centra bear conspicuous, forwardly converging vascular grooves, as in *Orycteropus*, and lack the prominent, paired, anterior and posterior tubercles present in manids. Lamberton reported that the faces of centra of the anterior caudals (including his "lumbar") are strongly inclined. The sacrum is decidedly orycteropodid, differing from that of the manids in numerous characters. The number of vertebrae, seven, is high, but only the first two are significantly involved in the pelvic attachment;[2] the width of the bone decreases across the middle vertebrae and increases again posteriorly, decidedly more so than in *Orycteropus*; there is no direct sacroischial connection, and the transverse process of the last pseudosacral does not form a heavy, blunt process projecting laterally beyond the dorsal rim of the ischium. The spines of the anterior sacrals are slight, low, largely fused and strongly inclined posteriorly, those of the posterior are larger, less fused and upstanding. The zygapophyses of sacrals 2 to 6 are not prominent.

Anterior extremity. It is in the structure of the limb bones, both fore and hind, that *Plesiorycteropus* differs most notably from the other members of the family, although differences from the pangolins are even more impressive. In the humerus the deltopectoral area is of orycteropodid, rather than manid, type, and the medial epicondyle is not drawn out into a long, bluntly pointed process. The radius is the most manid-like bone in the *Plesiorycteropus* body, a resemblance brought about by the hypertrophy of the linea obliqua and the transverse (not anteroposterior, as stated by Lamberton) flattening of the shaft. Both can be regarded as exaggerations of features present in other orycteropodids, however. Absence or very slight development of the radial tuberosity is a point of resemblance to manids. The distal articulation is greater in the transverse than in the anteroposterior diameter and is divided by a shallow groove; in both respects the resemblance is to the Orycteropodidae and not to the Manidae.[1] The ulna differs radically from that of other orycteropodids and of manids in the distal diminution of the shaft, which terminates in a small, styloid process bearing a facet for the cuneiform only. The large olecranon is straight, whereas in *Orycteropus* it is moderately and in manids more deflected medially. The groove in the lateral face does not terminate proximally in a fossa as it does in manids. Among the materials available to Lamberton were three kinds of metapodials, which he identified, with some hesitation, as Mc. II, IV and V. If he was correct, and I believe he was, then IV is longer relative to II and V longer

[1] The vertebra described and figured (pl. 4, figs. 13, 13[1], 13a) by Lamberton as a lumbar is an anterior caudal.

[2] Lumberton stated that *Orycteropus* has seven sacrals. This is possibly a lapsus, but he may have had an exceptional specimen. He also mentioned an ankylosis with the ilia in *Plesiorycteropus*; his figures do not support this, and the Paris fragment proves the contrary.

[1] Lamberton was not explicit as to whether or not the groove traverses the articular surfaces; in other orycteropodids the division is partial, not reaching the anterior border.

relative to IV than in *Orycteropus*. Other differences are to be seen in the smaller carpal articulations, the curvature of II and IV, the somewhat expanded distal ends of these bones and the limitation of the keels on their distal articulations to the plantar surfaces. In none of this is there any approach to the short, squat metacarpals of the manids. Lamberton suspected that Mc. I was lacking, as in orycteropodids and in contrast to manids, and in this he was probably right. One proximal phalanx is known and this is long and orycteropodid-like. The unguals are long, deep and bear a large plantar tuberosity. They are apparently more compressed laterally than those of *Orycteropus*, a point of resemblance to *Myorycteropus*. They differ from those of manids in not being fissured.

Posterior extremity. The pelvis is relatively shorter than in *Orycteropus* and has a rather "squared-up" appearance when viewed from above or below. The ilium is not expanded dorsally to any extent. There is some similarity to *Manis* in these features, but the basic structure is orycteropodid, as Lamberton noted. The outwardly curving ilium does not terminate anterolaterally in an expanded, blunt area, the ischium is concave medially above the obturator foramen, the pubis is directed medially as well as ventrally and posteriorly so that much of the acetabulum is visible in ventral view, the acetabular notch is wide and deep and the several processes —ischial tuberosity and spine, pectineal process, tubercle for M. rectus femoris—are well developed. The area around the ischial tuberosity is much more compact, and the ischium as a whole shorter than in *Orycteropus* as the preacetabular portion of the innominate is longer than the postacetabular. A decided point of resemblance to *Orycteropus* and of contrast to manids is to be seen in the stout, laterally projecting process from the area of the greater tuberosity. In *Plesiorycteropus* the process arises from this area; in *Orycteropus* it is anterior to the area, left behind so to speak as the ischium expanded posteriorly. Unfortunately, it is not clear from published accounts what muscle or muscles attached to the process. The sacroiliac articulation is set well forward, and is wholly anterior to the tubercle for M. rectus femoris rather than largely medial to it as in other orycteropodids. The femur is distinctive, having a small head set on a well differentiated neck, a very high great trochanter, no pectineal tubercle and a relatively enormous second trochanter that merges distally with the center of the posterior surface of the shaft. There is a certain resemblance to the rodent femur in all this, so much so that Grandidier (1912) described one of these bones as the type of his *Hypogeomys boulei*. Lamberton pointed out that a number of these femora had been found in various deposits together with pelves and lower leg bones, "with which they accord perfectly," and, just as tellingly, that no other bones of appropriate size that could represent a very large rodent have ever been found in Madagascar. His conclusion that the bones are attributable to *Plesiorycteropus* seems inescapable. The femur agrees with that of the manids in the possession of a wide, shallow rotular groove and in the lack of a pectineal tubercle but otherwise differs decidedly in the possession of a medianly placed third trochanter,[1] a deep digital fossa and a large pit in the head for the ligamentum teres, characters present in orycteropodids. The neck of the femur in *Myorycteropus* is better developed than in the living form. At first glance, the tibia and fibula look rather peculiar, but careful examination reveals that the peculiarity, from an *Orycteropus* point of view, is mainly due to three things: the lateral compression of the proximal half of the tibia, the prominent tubercle at the distal

[1] In Tertiary manids (Emry, 1970: 498, fig. 30) the third trochanter progressively moves distally until in the living forms it disappears and M. gluteus maximus comes to insert on a swelling above the lateral condyle.

end of the cnemial crest, and the extensive distal fusion of the two bones. As regards the fusion, due to ossification in the interosseous membrane, *Plesiorycteropus* has simply carried to conclusion a tendency latent in the family (cf. Fig. 13). *Myorycteropus* approaches the Malagasy form in its possession of a cnemial tubercle and a compressed proximal portion of the shaft. The structure of the manid tibia and fibula, which never fuse either proximally or distally, is very different. The astragalus of *Plesiorycteropus*, conforming to the short, comparatively shallow, distal articulation of the tibia, is short proximodistally, with the head and the relatively short neck directed much more medially than in *Orycteropus* and *Myorycteropus*; an astragalar foramen is lacking and the trochlea is shallower. The facet for the internal malleolus of the tibia is comparable to but better developed than that of these two forms; it extends medially on to the neck and is shaped to receive the forwardly facing part of the articular surface of the malleolus. The head, although convex, is less rounded than in *Orycteropus* and the navicular facet extends farther proximally on the medial side. The manid astragalus also lacks a foramen, at least in the living forms,[1] but is otherwise quite dissimilar. The neck is long and directed distally, and the head is largely concave. The manid tibia has no internal malleolus, strictly speaking, and hence there is no medial facet on the dorsal side of the astragalus.[2]

To sum up, it would appear that *Plesiorycteropus* displays few resemblances to and many differences from the Manidae. Such similarities as exist are not of a kind that would suggest relationship. On the other hand, there is a pervasive similarity to the Orycteropodidae, which is most evident in the axial skeleton and pelvis, less so in the leg and foot bones. Even in these, however, the basic structure on which the various specializations have been superimposed is an orycteropodid one. I believe there can be no doubt as to the ordinal affinities of the Malagasy form.

PHYLOGENY AND MAJOR TAXONOMY

The Tubulidentata are sometimes cited as an example of an essentially monophyletic order. As *Plesiorycteropus* plainly demonstrates, such is not the case. Furthermore, in addition to this major cleavage within the group, it is now apparent that the African and Eurasian genera, while closer to each other than to the Malagasy one, do not stand in any ancestor-descendant relationship. Each of them represents a distinct lineage.

Leptorycteropus, tooth structure apart, is a rather primitive eutherian. While recognizeably an orycteropodine, it is less specialized than the other forms. Structurally it could represent the ancestry of *Orycteropus* and *Myorycteropus*, but its late survival indicates that its predecessors had been independent of theirs since at least Oligocene time.

Orycteropus makes its earliest certain appearance with *O. mauritanicus* of the "Vindobonian" of Algeria. This is a smaller species than the living one, and, as Arambourg emphasized (1959: 46), all the known limb bones are somewhat more slenderly constructed. This is also true of the yet smaller *O. gaudryi*. From available evidence it would thus appear that there has been a modest and late increase in overall robustness of the limb bones, together with reduction of Mc. V and the fifth digit of the pes, and a relative increase in the size of the manus within *Orycteropus*. Progressive enlargement of the olfactory area and lengthening of the facial region occurred.

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[1] Grassé (1955: 1273) unaccountably stated it to be present; it is known only in an unnamed Aquitanian specimen referred to the order by Helbing (1938: 300).

[2] There is a posteromedial styloid process, separated by a groove from the medial side of the bone, but this articulates with the astragalar trochlea, which continues proximomedially to the plantar surface.

An increase in body size accompanied by a proportionately smaller increase in head size is also evident. *O. afer* is about twice as large as the known species of the other genera, and even the comparatively small *O. gaudryi* is decidedly larger. Relationships between the described species of *Orycteropus* are not clear. Tubulidentates first reached Eurasia at some time in the Miocene (assuming an African origin for the order, see p. 232) and there may have been independent evolution within the genus in the north. I doubt if *O. gaudryi* was involved in the ancestry of *afer*, which conceivably could have come from *mauritanicus*, but whether *depereti* descended from *gaudryi* or, as such, reached Eurasia from Africa is uncertain. Progress here must await discovery of more complete materials in both continental areas.

Compared to *Orycteropus*, *Myorycteropus* is precociously specialized for digging and, as MacInnes stresses, could not have been involved in the ancestry of the living genus. The fossorial features present in the fore legs of the latter are by no means as pronounced as those of *M. africanus*. The known bones of the manus of the early Miocene form are relatively larger than those of *O. afer*, not to mention *O. gaudryi*, and Mc. V is relatively long. Specializations apart, however, the structure of the fore limb is basically similar in *Myorycteropus*, *Orycteropus* and *Leptorycteropus*. In the hind limb the femur and tibia stand somewhat apart in structure from those of *Leptorycteropus* and the living form.

In summary, both the *Orycteropus* and the *Myorycteropus* lineages trended toward acquisition of a fossorial habitus, but they did so in somewhat different ways at different times, the *Myorycteropus* lineage going farther in this direction at an earlier date, at least as regards the fore limb. The *Orycteropus* and *Leptorycteropus* lineages may be more closely related to each other than either is to the *Myorycteropus* one.

As sufficiently emphasized above, *Plesiorycteropus* stands far apart from the other members of the family, so much so as to leave little doubt that its ancestry has had a long independent history. Mahé (1972: 356) suspected that its predecessors may have reached Madagascar sometime in the Eocene, at about the same time as the ancestral lemuroids arrived there. I would agree.[1] Evolution within the *Plesiorycteropus* lineage has resulted in a terminal form so distinctive as to merit subfamilial distinction. This taxon may be defined—and contrasted with the Orycteropodinae—as follows:

Plesiorycteropodinae subfam. nov.

Skull with short facial region, no postorbital process, glenoid articulation low, on ventrally directed process of squamosal. Sacrum with seven vertebrae, relatively narrow anteriorly and wide posteriorly. Humerus with deltopectoral area confined to proximal half of shaft and inclined laterally, supinator crest evenly decreasing proximally, medial epicondyle not greatly expanded proximodistally. Shaft of radius much compressed transversely, linea obliqua very salient. Ulna decreasing markedly in size distally, articulating only with cuneiform, olecranon long, straight. Metacarpals with keels of distal articulations limited to plantar surfaces, proximal ends of Mc. II and Mc. IV small, Mcs. IV and V not notably reduced in length relative to Mc. II. Pelvis relatively short, ischium with very large tuber ischii, area of sacral attachment situated well forward, anterior to level of large, elongate, crested tubercle for M. rectus femoris. Femur with small head; well defined neck; large, high great trochanter; large second trochanter extending far medially, merging distally with center of shaft; third tro-

[1] He also suggested that the ancestors of *Cryptoprocta* crossed at about the same time. Here I must differ and concur with those (e.g. Cooke, 1972: 125) who regard as probable a late Oligocene or early Miocene date for the arrival of viverrids in the island.

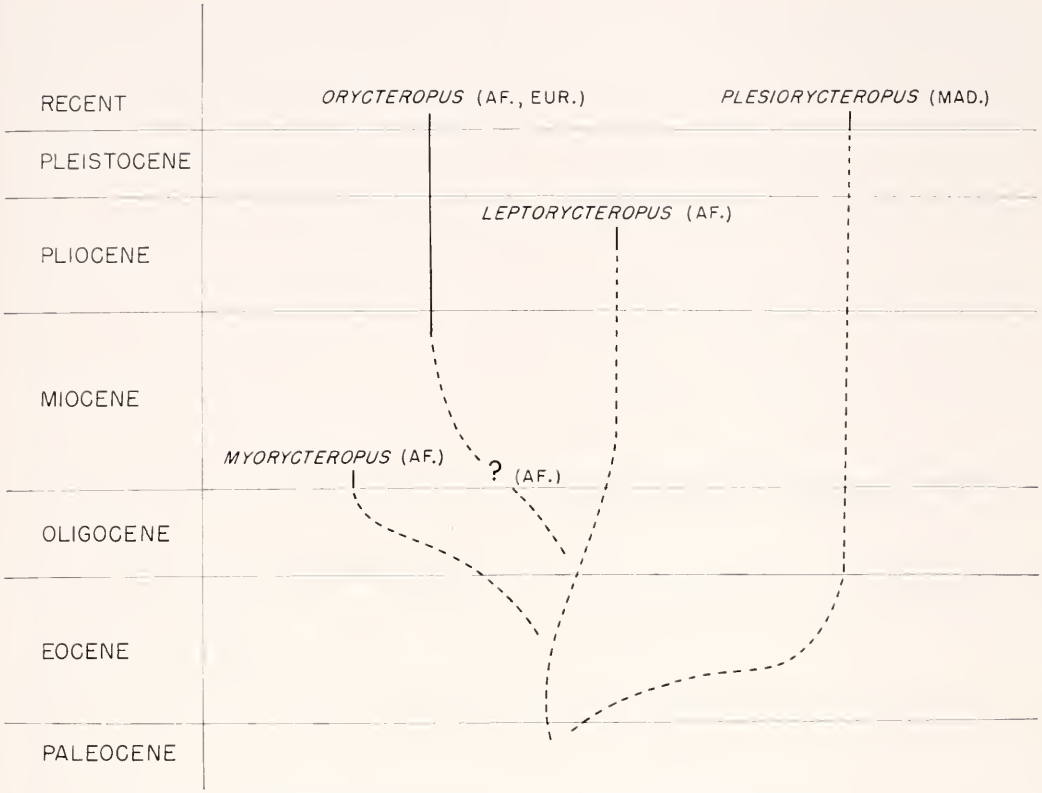

Figure 16. Suggested relationships of the known tubulidentate genera.

chanter merging proximally with crest running from great trochanter; shallow rotular groove. Tibia-fibula fused distally as well as proximally, distal articular surface short anteroposteriorly, proximal portion of tibia compressed laterally. Astragalus short proximodistally, neck short and inclined medially, facet for internal malleolus of tibia large, foramen lacking.

Sole known representative: *Plesiorycteropus madagascariensis* Filhol 1895; Recent superficial deposits, Madagascar.

Figure 16 presents an interpretation of tubulidentate phylogeny that seems reasonable on the available evidence. The plesiorycteropodines, be it noted, as descendants of waif immigrants from Africa, are a splinter group from, *not* the "sister group" of, the Orycteropodinae.

ADAPTATION AND BEHAVIOUR

Orycteropus afer

The living aardvark is a nocturnal animal and hence difficult to observe, a difficulty compounded by its partially subterranean habits. Nevertheless something, although by no means enough, is known of its biology (Fitzsimons, 1920: 233–247; Frassati, 1937; Bigourdan, 1950; Hediger, 1951: 61–73; Verheyen, 1951: 94–98; Urbain, 1954; Verschuren, 1958: 89–100; Rahm, 1961b; Kingdon, 1971: 376–387; Pagès, 1970).

An inhabitant primarily of savanna grasslands, although extending into forested (Rahm, Pagès) and more arid areas, it is a powerful digger that constructs burrows in which the daylight hours are spent.

Verheyen records that after a cold night an individual may sun itself outside the burrow during the early morning hours; aardvarks lack an insulating layer of subcutaneous fat. The temperature and humidity within the burrow during the day are essentially the same as those at the surface of the ground during the night (Verschuren). The animal digs a burrow with great rapidity, excavating with the fore feet and shifting the earth back by powerful movements of the hind feet and tail. An aardvark enters its burrow head first; accounts of its method of exit vary. Bigourdan described it as first poking its head out of the entrance, listening and sniffing the air, then bounding a short distance and repeating the process, and finally bounding in a semicircle around its hole before moving off. Harroy (reported in Verschuren) observed an individual emerging stern first, thrashing its tail about and stirring up clouds of dust as it did so. When hard pressed within the burrow an aardvark can literally erupt out head first from a new opening (Verschuren). Its fast gait is bounding but not rapid; Urbain so described it, but he was apparently observing aardvarks dashing from one hole to another. Shortridge (1934: 66) has stated that: "On suspicion of danger, the Ant-Bear—like the Pangolin—is in the habit of raising itself on its hind quarters and gazing [sniffing, surely] around, sometimes even shuffling along in this position, balanced by its stout kangaroolike tail." Fossati has observed similar behaviour.

Escape from mammalian predators—lions, leopards, hyaenas, dogs—is accomplished mainly by digging, and the burrow also serves as a protection from grass fires, at which times aardvarks play host to a wide variety of uninvited guests, ranging from arthropods through frogs, lizards and snakes to those mammals who can enter. Fitzsimons wrote of aardvarks dealing adversaries powerful blows with their shoulders by means of rapid and sudden turning movements. Kingdon remarked that "... when attacked by dogs it has been seen to turn a somersault. This effectively throws off the attackers, after which it proceeds throwing somersaults whenever touched." Sometimes, he goes on to note, an aardvark will do this when only startled. Behaviour of these kinds would serve to gain time for digging. In an extremity it may, so Verheyen records, throw itself on its back and prepare to defend itself with all four feet.[1] That this reaction is not universal is attested to by Fitzsimons who once observed an aardvark attacked by a leopard: "The intended victim bunched its body up, and keeping its head out of harm's way between its front legs, it shook the Leopard off repeatedly, and actually dug itself into the earth and escaped." He further remarks that in leopard infested districts "..... sometimes the entire back is a mass of healed scars inflicted by the teeth and claws of a Leopard." Accounts of the thickness of the skin are surprisingly conflicting. Hedinger describing it as thin—"... je fus frappé par le minceur et la souplesse de la peau (pas de tout genre couenne!)"—and Fitzsimons going to the opposite extreme: "... skin ... thick, tough and fibrous, and the blade of penknife will usually snap if an attempt is made to drive it through ...." For me, at any rate, the matter is set at rest by one of the earliest studies of the anatomy of *Orycteropus*. Jäger (1837: 12) described the skin as "... überall sehr stark und an manchen stellen ½″ dick, ähnlich der der Pachydermen ...", and added, in agreement with an observation made over a century later by Verheyen, "... sie war durch ein dünne Lage sehr dichten Zellgewebes mit dem Hautmuskel verbunden."

It has been reported (Verheyen) that aardvarks in the course of their nightly wanderings are capable of covering distances of between 10 and 30 kilometers, and

[1] Kingdon, but no one else, states that it will stand erect and strike at an adversary with the claws of the fore feet in the manner of the myrmecophagids.

may return to a former burrow or construct a new one at daybreak. The animal is fully capable of swimming. Aardvarks, especially the males, are solitary for parts of their lives. Males and females consort in the same burrow during the mating season and the one (rarely two) young remains with the mother for six months or so after. Smell and hearing are the dominant senses.

All accounts agree that the primary food of aardvarks in the wild consists of termites and, to a much lesser extent, of ants, although, in common with other myrmecophagous mammals, they vary their diet to some degree (p. 226). *O. afer* exploits the large ground termite nests that form so conspicuous a feature of the tropical African landscape, its area of distribution, according to Grassé (in Pagès), almost exactly corresponding to that of the Macrotermitinae. Aardvarks make excavations 30 cm. wide and 40 deep in the sides of the hills, and may drive even deeper holes into the interiors (Verschuren), to a depth of 3 meters or more (Pagès). According to Bigourdan, the aardvark rotates its visits to nests, following a circuit of 2 to 4 kilometers around its burrow and visiting individual hills at intervals of 5 to 8 days, thus allowing the colonies, whose powers of recuperation are immense, a rest between raids. As he observed, the relationship is amusingly reminiscent of that of a bee keeper to his hives. Pagès, on the other hand, reports destruction of nests due to repeated visits.

On the evidence there can be no doubt that *O. afer* is a well-adapted, fully committed myrmecophage. The several extinct species of the genus in all probability resembled it in most behavioural respects, at least their known hard parts strike no discordant note. Within the genus there was certainly an increase in the digging capability and there may have been some increase of the olfactory sense. As befits an animal apparently capable of detecting fruits and grubs 30 cm. or more underground, *O. afer* is highly macrosmatic. It has 10 endoturbinals (including the nasoturbinal)[1], the highest number recorded in the Mammalia, and richly developed ectoturbinals, which, again, are more complex than in other mammals (Coupin, 1926). The sinus system within the skull is extensive, with all components except the sphenoidal intercommunicating to form what Coupin calls the "sinus générale", into which the ectoturbinals extend. In *O. gaudryi* the ethmoidal area and the "sinus générale" are less expanded than in *afer* (cf. figures in Colbert, 1941, especially 21). *O. depereti*, to judge from Helbing's figures, is somewhat more advanced than *gaudryi* in these respects, which suggests that the turbinal system, especially the ectoturbinal portion, was enlarging.

To what extent may the extinct genera have resembled *Orycteropus*? Before taking up the question, the nature of the myrmecophagous adaptation requires consideration.

The Myrmecophagous Adaptation

Ants first appear in the fossil record in early late Cretaceous time and termites in the mid-Cretaceous; since the earliest known termite, a hodotermitid, is not a member of the primitive family Mastotermitidae the origin of the order obviously goes back to an earlier date (Wilson, 1971: 31, 105–8). The colonies of numerous termite and of some ant species are enormous, with individuals numbering in the hundreds of thousands and even millions (Wilson, 1971: 436–9). The highly successful radiations of these two great groups of social insects, which approximately coincide with those of metatherian and eutherian mammals, have made available rich, concentrated sources of food. Among the vertebrates, numerous omnivorous, insectivorous and carnivorous forms take advantage of this resource, the majority of them

[1] Weber (1904: 416) reported 11 and Le Gros Clark (1926) 9; Coupin found 10 in each of twelve specimens.

opportunely by taking foragers or alates during nuptial flights.[1] To penetrate to the interiors of the colonies, to tap the riches at their source and to depend upon them as the major articles of diet—in other words to become a fully committed myrmecophage—requires the evolution of special equipment.

The nature of this equipment has been admirably summarized by Griffiths (1968: 230–246). In brief, in eutherian mammals, it consists of a very extensible, vermiform or ribbonlike tongue lubricated by sticky secretions from greatly enlarged salivary glands, a highly developed olfactory sense, a stomach with a very muscular pyloric area that acts as a "gizzard" for grinding the food, and limbs of fossorial type to breach the walls of nests. In the echidnas there is no specialization of the pyloric area, the food being ground by the spiny base of the tongue acting against spines on the palate. As usual when convergent evolution is involved, the adaptive complex has been attained in somewhat different ways in the several myrmecophagous groups, but the function of the whole is similar throughout. It is a device for the rapid transfer of small prey to the stomach in large quantities—Griffiths (1968: 40) reports that an "echidna of about 3 kg. weight can ingest 200 g. wet weight of termites . . . in a matter of 10 min."

Teeth are superfluous to the adaptation. With the conspicuous exception of *Orycteropus*, fully committed myrmecophagous mammals have either lost their teeth entirely (echidnas, pangolins, myrmecophagids) or have reduced them greatly (*Stegotherium* and, probably, *Plesiorycteropus* and the myrmecophagous palaeanodont *Patriomanis*—Emry, 1970: 468). The masticatory musculature in these forms is accordingly much reduced, with accompanying reduction of the temporal fossa, postorbital process and, in some cases, the zygomatic arch. The ramus of the jaw becomes diminished to a straight or nearly straight rodlike structure with little or nothing by way of an ascending portion, and the condyle and glenoid articulation are in one way or another brought down nearly or completely to the level of the palate. This combination of osteological characters (cf. Anthony, 1929), together with a median groove in the bony palate (not present in myrmecophagids), permits ready recognition of any extinct myrmecophage possessing it, but it must be observed that on these criteria one could not be sure that *Orycteropus* was a committed myrmecophage were it known only in the fossil state. The genus has fully functional molars and posterior premolars and a high ascending ramus, which resembles, as Frechkop (1937:18) has noted, that of the camels; it stands in striking contrast to *Plesiorycteropus* with its rather pangolin-like jaw articulation. This very curious anomaly is discussed below (p. 226).

There would appear to be at least two avenues of approach to full myrmecophagous specialization: either from fairly generalized insectivorous-carnivorous ancestors or from insectivorous-omnivorous ancestors with moderate to marked fossorial adaptation. In either case an increasing dependence on termites and ants for food would have provided the base for further specialization. (An ability to extend the tongue and to scratch or scrape earth—the essential requirements for a beginning—are of course characteristic of terrestrial mammals generally.) Certain living forms illustrate these approaches.

Myrmecobius fasciatus, the numbat (Fleay, 1942; Calaby, 1960), is an example of the first. Termites constitute its main diet, with ants forming about 15 percent; Calaby suspects that most of the latter, together with the very small beetles whose

[1] Once, rounding a corner in Turkana, I came upon a towering termite hill in full nuptial eruption at midday. Gathered about was a variety of birds, ranging, to my surprise, up to hawks and eagles, all eagerly feasting on the temporary bounty provided by the myriads of alates on the ground in the vicinity of the nest.

remains are sometimes found in the seats, are taken together with the termites. The animal "... appears to swallow its food without chewing," (Calaby). Fleay observed that a captive specimen did chew large termites, but Calaby notes that such species do not occur within the numbat's present range. Concordant with this degree of dietary specialization, the tongue can be extended for approximately 100 mm. (condylobasal length of skull 54.0 to 58.3 mm.—Tate, 1951), the facial region is elongated, the palate is long, unfenestrated and grooved medially, the mandible is moderately, although not extremely, reduced and the cheek teeth, evidently little used, are notorious for their variability (as Calaby remarks they seem to be escaping from selection pressure). On the other hand the stomach displays no modification in the pyloric area and the limbs lack fossorial specializations other than some enlargement of the fore claws (Griffiths). The numbat seeks its food by scratching in the upper few inches of the soil or by turning over pieces of wood. It does not attack nests except to scratch in their upper surfaces when these have been softened by rain. Grinding of the food in the stomach is no doubt aided by coarse sand ingested with the prey.[1] *Myrmecobius* is an animal in transition—an "amateur anteater" in Griffith's words—that could be on the way to full commitment, or "professional" status. It has attained a morphological threshold at which any genetic changes leading to pyloric thickening, further fossorial specialization, etc., would be selectively advantageous.

The aardwolf, *Proteles cristatus,* has also gone some distance along the route to myrmecophagy. It subsists very largely on harvester termites (*Trinervitermes*), although other insects, carrion, small vertebrates and vegetable food have also been recorded as items in the diet (Ewer, 1973: 204, 205). The small, peglike cheek teeth are reduced and variable in number ($\frac{4-3}{4-2}$) and display little wear in specimens available to me. Stomach structure is consistent with this reduction, the walls being "very thick and muscular, especially towards the pyloric end" (Flower, 1869:486). For the rest, *Proteles* would seem to be less modified in response to myrmecophagy than *Myrmecobius.* The tongue is apparently not notably protrusile. Rather surprisingly, in view of the greatly reduced cheek teeth, the lower jaw is strongly built, with a high coronoid process, and the postorbital process is prominent. The canines, however, are large, somewhat peccary-like teeth that develop extensive mutual wear surfaces. As Ewer has suggested (p. 60), retention of a strong masticatory musculature and associated bony structures may be related to use of these teeth, perhaps for defense—and, it may also be supposed, for killing small vertebrates. The feet are not adapted for proficient digging—there is less disparity in size between the unguals of the fore and hind feet than in *Myrmecobius*—and the animal is not able to open termite mounds (harvester termites, the principal food item, forage very extensively on the surface of the ground and are hence readily accessible).[1]

Examples of the second and, I suspect, more usual avenue of approach are provided by the armadillos, a family that had evolved a fully committed myrmecophagous representative, *Stegotherium* (Scott, 1903: 12–40; 1937: 680), by early Miocene time. The Dasypodidae are in the main fossorial and omnivorous, and ants and

[1] This naturally happens with any terrestrial myrmecophage but grit is not essential to comminution in the fully committed ones with "gizzards", as is shown by the fact that small pebbles are only rarely encountered in the stomachs of the arboreal forms that attack colonies of tree-nesting termites.

[1] In its retention of strong canines and relatively robust mandible *Proteles* resembles the Eocene palaeanodont *Metacheiromys.* The latter and its relative *Palaeanodon* have median palatal grooves, which suggest possession of extrusible tongues, and their cheek teeth are greatly reduced. These fossorial forms may have subsisted to a considerable degree on termites.

termites are known to be eaten by some of them. The only species whose food habits have been studied in any detail is *Dasypus novemcinctus*. From field observations and analyses of the stomach contents of 169 individuals collected over 10 months of the year in Texas, Kalmbach (1944: 15–18, 23–50) found that 488 species contributed to the diet. Animal food averaged 93.3% of the stomach contents, vegetable food 2.1% and vegetable debris, presumably ingested with the prey, 4.6%. Invertebrates averaged 91.7% and vertebrates 1.65%, with insects forming 77.6%, arachnids and myriapods 7.9%, and miscellaneous invertebrates (worms, molluscs, crayfish) 6.2%. Beetles, 41.6%, form the major article of diet, with one family, Scarabeidae, contributing 27.9% to the whole. Hymenoptera, mainly ants, form 14% and termites 4.5%. Enormous numbers of termites and ants may be taken, however. One stomach contained "at least 40,000 ants of several species" and another "some 13,000 termites." The vegetable food consists of fruits, berries, mushrooms and seeds, although some of the latter may have been ingested accidentally; Kalmbach remarks (p. 52): "Field observations indicate that under some conditions armadillos may subsist on vegetable matter to a far greater extent than has been disclosed by stomach examination." Among the vertebrate food items are salamanders, frogs, lizards and their eggs, small snakes and snake's eggs, young birds and bird's eggs, young rodents and rabbits, and carrion. "Small insects are swallowed whole and unmutilated and many of the larger but soft bodied creatures such as cutworms, earthworms and some beetle larvae are handled in the same manner. Larger hard-shelled insects, and salamanders, lizards and batrachians are subjected to a chewing process, and their remains in the stomach usually are mutilated if not dismembered. Vegetable items including berries and mushrooms are subjected to considerable mastication before being swallowed" (p. 18). Young rabbits are " . . . killed and mutilated by thrusts of the . . . front feet . . . actual eating was accomplished by continued chewing until the food was softened and torn enough to be swallowed" (p. 44). Eggs if small enough are taken entire and crushed in the mouth; if too large they are broken by the claws and the contents lapped up. The percentages of the various prey groups that make up this highly varied diet change with the seasons—and no doubt over the range of the species. In the tropics *D. novemcinctus* probably consumes a higher percentage of termites, although data are lacking.

The scattered and scanty information available on the diets of other armadillos reveals food items similar to those recorded for *D. novemcinctus*, e.g., beetles, termites, ants, maggots, caterpillars, worms, small snakes, carrion, vegetable matter, etc. *Dasypus* and *Cabassous* do dig for ants and termites (Kalmbach; Ingles, 1953: 268) and take them with their moderately extrusible tongues. The salivary glands extend back along the underside of the neck (Kühlhorn, 1939: 81). The pyloric areas of the stomachs of *Dasypus*, *Euphractus* and *Tolypeutes* are known to be somewhat thickened (Owen, 1831: 142, Kalmbach, 1943: 28–29; Owen, 1832: 155; Murie, 1874: 86), although evidently not to the extent seen in a committed myrmechophage. Nevertheless, such thickening would aid in the comminution of prey items swallowed whole and in the further reduction of those chewed. The arrangement in fact exemplifies the essential base from which, in eutherians, the transfer of the grinding function from the teeth to the pyloric "gizzard"[1] could progressively proceed.

[1] A highly muscular pylorus is not confined to myrmecophagous forms among the Mammalia, although, apart from them, it is very rare. Böker (1937: 177), who calls stomachs of this type Kaumagen, records them as occurring in certain squid eating odontocetes and in *Dugong*. Such a structure is also present (Davis, 1964: 207), in conjunction with very large, crushing cheek teeth, in the Giant Panda, *Ailuropoda melanoleuca*, which feeds on bamboo shoots.

None of these three armadillos is committed to myrmecophagy to any great extent—much of their food is chewed, their jaws are not reduced, their glenoid articulations are rather high on the skull, and their teeth do not exhibit the marked variability that accompanies loss of function. Nevertheless such forms as *Dasypus*, *Cabassous* and *Tolypeutes* would appear to stand poised near the beginning of the road to it.

The living species that seems to have gone farthest toward myrmecophagy is the giant armadillo, *Priodontes maximus*. Little is actually known of its feeding habits. Accounts of stomach contents record caterpillars, beetle larvae, maggots and worms (Kappler in Heck, 1920: 520), but the animal is reputed ("... verschiedener Beobachter berichten . . . "—Kühlhorn, 1939: 59) to be very partial to termites. Several anatomical features are to an extent consistent with this. The animal is a very powerful digger that constructs burrows; as such it could make short work of termite hills. The tongue is vermiform and can be extruded for a considerable distance—Kühlhorn found that in a recently dead individual it could be pulled out some 160 mm (length of head 172–200 mm—Krumbiegel, 1940: 54); the salivary glands extend back to the sternum. Nothing is known, apparently, about stomach structure; it would be interesting to learn if the thickening of the pyloric area has gone beyond that encountered in other armadillos. The glenoid articulation is low on the skull, not as low as in the Miocene *Stegotherium* but lower than in other living armadillos, and the posterior portion of the mandible has undergone some reduction. The numerous teeth, small in proportion to the size of the skull, are highly variable in number; in the upper jaw they fluctuate between 14 and 20 on a side and in the lower between 17 and 21[1] (Kühlhorn, 1939: 76). Like those of *Myrmecobius*, they may be escaping from selection pressure. As Kühlhorn concluded, the giant armadillo stands part way between the omnivorous *Dasypus*, *Cabassous* and *Tolypeutes* and the fully specialized myrmecophagous xenarthrans. (*Stegotherium*, one of these, is related to *Dasypus*, while *Priodontes* is allied to *Cabassous* and *Tolypeutes*—[Patterson and Pascual, 1972: 265, fig. 6].) The animal is an "amateur" anteater to about the same extent as the numbat despite the different routes the two have followed and the different degrees of specialization each has attained in one component or another of the adaptation.

[1] I doubt if the acquisition of so great a number of teeth was in any way associated with myrmecophagy. Better knowledge of the behaviour and food habits of *Priodontes*, which has no fossil record, may provide a clue to their function.

The Extinct Orycteropodid Genera

Turning to what can reasonably be reconstructed regarding the adaptations of the extinct aardvarks, it can be said at once that *Leptorycteropus* was not specialized for myrmecophagy. What is known of the structure of the skull reveals nothing of the osteological combination associated with that method of feeding. The temporal fossa and postorbital and jugal processes are relatively well developed, the palate is not grooved, the mandible has an extensive, firm symphysis, and a rather large canine is present, together with a full complement of cheek teeth. The limb bones indicate an animal capable of digging but not highly specialized for it; *Leptorycteropus* may have dug its own burrows but was certainly not as proficient as *Orycteropus* in doing so. Like *Dasypus*, it may, in addition to going to ground, have escaped its enemies by quick dashes into dense thickets. A thick and tough hide, supposing this to have been common to the order, would, like the armadillo carapace, have protected it from plant spines and thorns. The impression conveyed is of an omnivorous form that was a faster runner than the living species. Like other omnivores it no doubt ate termites and ants, but was not dependent on them to a major degree.

Since *Leptorycteropus* had the characteristic tubulidentate tooth structure I would judge that acquisition of this had nothing to do with myrmecophagy. Like the dental structure of the Xenarthra it may have evolved early in the Tertiary.[1]

Myorycteropus was as far ahead of *O. afer* in fossorial adaptation as *Leptorycteropus* was behind it, at least as regards the fore limb. The pelvis and hind leg bones are not as robustly constructed as those of *Orycteropus* (Figs. 12–13), which suggests that the hind legs and tail were not as much employed in digging. In all probability it constructed burrows. It was beyond any doubt perfectly capable of attacking termite and ant nests, but its degree of commitment to myrmecophagy is at present impossible to assess. Nothing is known of the skull other than a maxillary fragment, and this is not complete enough to reveal whether or not a median groove was present on the palate. The ascending ramus of the mandible slopes posteriorly considerably more than does that of *Orycteropus* and the condyle is lower. On this very scanty evidence one might suspect that *Myorycteropus* was some way along the road, but there can be no certainty on this. The jaw, dentition aside, is not as a whole very different from that of *Dasypus*, and there is nothing to indicate that the diet of *Myorycteropus* could not have been comparably diverse. Only if remains of possible descendants are found in later Miocene or Pliocene deposits will it be possible to determine whether or not a trend toward marked reduction of the jaw and elimination of the dentition was under way in the lineage.

There is much less uncertainty regarding the diet of *Plesiorycteropus*. Alone among tubulidentates, it displays cranial characters associated with a definite commitment to myrmecophagy, of which the most significant is the carrying down, somewhat in the pangolin manner, of the glenoid articulation on a descending zygomatic process of the squamosal. This implies that the posterior portion of the ramus was much reduced and the teeth diminished or perhaps lost entirely. Whatever the factor or factors that operate to maintain the size of the mandible and the persistence of fully functional teeth in *Orycteropus* may be (see below), they were not involved in the evolution of the Malagasy form.

The leg bones differ in numerous respects from those of orycteropodines (Figs. 10–13) and exhibit points of similarity to those of other groups, especially to armadillos—and within that family to *Dasypus*. The similarities to this genus,[1] which include the general structure of the humerus, the long and straight olecranon, the relative lengths of the fore and hind leg bones and the general structure of the femur and the tibia-fibula, are striking. *Plesiorycteropus* was certainly capable of digging and hence of breaking into nests. In one character, the tapering distal end of the ulna, it differs decidedly from both armadillos and orycteropodines, but agrees well enough with other accomplished diggers, such as *Phascolomis* and *Marmota*. The very high great trochanter of the femur common to both *Dasypus* and *Plesiorycteropus* is a very interesting point of resemblance. Marked elevation of the trochanter above the head of the femur is a character encountered in various mammals that are proficient jumpers and in which the main propulsive force is supplied by the hind legs—the higher the trochanter the more rapidly contraction of

[1] The teeth of these two groups are often spoken of as degenerate. As far as loss of enamel is concerned this is true, but, as Röse (1892: 508), for one, has emphasized, in losing it they have attained new orders of specialization, involving hypselodonty and modifications of the dentine. One advantage of such teeth, which are well suited to herbivorous, omnivorous and insectivorous diets, is that they can rapidly adjust to the jaw movements of individuals, as may be observed in adequate series of various xenarthrans.

[1] The bones figured as *D. novemcinctus* by Emry (1970) are not of that species but of *Euphractus sexcinctus*.

M. gluteus medius can act in extending the femur (cf. Smith and Savage, 1956: 612–613). The very large size of the M. rectus femoris origin may also be interpreted as indicating jumping abilities (cf. Gazin, 1968: 63). Kalmbach recorded that *D. novemcinctus* frequently jumps upward when disturbed. This is a useful defensive reaction. I have seen, in motion pictures taken in the Venezuelan llanos under the direction of Dr. R. Marlin Perkins for the television series "Wild Kingdom", two individuals of *D. novemcinctus* being harassed by a couple of bush dogs (*Speothos venaticus*). The armadillos were paying little attention to them, but whenever the activities of the dogs became too annoying they would jump straight up, spilling their tormentors. In more serious situations such behaviour would gain time for a dash to safety—and *Dasypus* is capable of good bursts of speed over short distances (Roosevelt, 1914: 85). A capacity for jumping no doubt also serves *Dasypus* well in the course of its daily rounds.[1] I suspect that much of the behaviour of *Plesiorycteropus* on the ground was similar to that of the armadillo.

At all localities yielding its remains *Plesiorycteropus* occurs together with various lemurs, some of which are or were arboreal. At least one of these localities, Ampasambazimba, was situated in a densely forested area at the time the sediments there were deposited (Tattersall, 1973a: 10–16, 24). Could *Plesiorycteropus* have been at least partially arboreal, as Lamberton (1946: 47), in describing the unguals, seems to have thought? Simpson (1931: 315–319), calling attention to osteological characters possessed in common by various fossorial and arboreal mammals, pointed out that a shift from one habitus to the other could readily occur. Certain living myrmecophagous mammals exemplify this. Among both anteaters and pangolins intermediates between one habitus and the other exist. *Tamandua* is both arboreal and terrestrial, attacking tree and ground termite colonies, while *Myrmecophaga* is terrestrial and *Cyclopes* arboreal. Of the manids, *Phataginus tetradactyla* and *P. tricuspis* are primarily arboreal, excellent climbers that sleep in trees (Pagès) while other species sleep on the ground in burrows or holes. Of these, *P. gigantea* is almost exclusively terrestrial, but some, e.g., *P. temmincki* and *Manis pentadactyla,* are also capable of climbing and of attacking tree colonies (Rahm, 1961a). There is nothing in the known parts of *Plesiorycteropus* that would rule out a similar capability. The humerus resembles that of the arboreal phalangers as well as that of *Dasypus.* The lack of expansion of the distal end of the ulna would be consistent with, although not necessarily evidence of, climbing habits. The rather shallow crurotarsal articulation, together with the shape of the astragalus and the medial extent of its navicular facet (cf. *Phascolarctos*), suggest a foot less confined than those of orycteropodines to movements in the sagittal plane. Fusion of tibia and fibula is no bar to arboreal habits (cf. myrmecophagids), and an ability to jump would be advantageous. The termite fauna of Madagascar includes tree as well as ground nesting species (Paulian, 1970: 289–290); *Plesiorycteropus* could have taken advantage of both. It may well have been the most versatile of the aardvarks.

The tubulidentates were evidently more varied in adaptation and behaviour than has been supposed. As concerns the locomotor apparatus the order included forms both less and, in the fore limb, more fossorial than the living representative and one that seems to have been partially arboreal. As regards diet, at least one and possibly two were omnivores, and two otherwise differently adapted lineages in-

[1] And in unusual situations too. Once, while a guest in a household that included two partially grown *D. novemcinctus,* I heard a clatter one morning and on investigating found that the pair had jumped up on the dining room table where they were happily consuming the breakfast.

dependently evolved to full myrmecophagous commitment, each, I suspect, via the second or "armadillo route" to that specialization. It begins to appear that aardvarks played roles in Africa and Madagascar analogous to those of the armadillos and anteaters in South America. (Pangolins, on the other hand, may have been more circumscribed by an early commitment to myrmecophagy, but their fossil record is unfortunately too scanty to throw much light on the matter.) During the early Tertiary tubulidentates were perhaps more numerous and diversified than during the later. Earlier they would have encountered little competition in the omnivore zone, and their only mammalian predators then were hyaenodontid creodonts in Africa. With the arrival of the Carnivora around the end of the Oligocene they would have been faced not only with new predators but in all likelihood with direct competition as well. A number of the smaller Carnivora of present day Africa are insectivorous-omnivorous, and some are fossorial in addition (Bigalke, 1972: 161–166); conditions in the later Tertiary may well have been similar.

The Retention Of Functional Teeth in Orycteropus

The intriguing question as to why *Orycteropus*, alone among committed myrmecophagous mammals, should possess fully functional cheek teeth and a high ascending ramus remains for consideration. The masticatory musculature (Edgeworth, 1924; Sonntag, 1925: 339–340; Frick, 1951) is of the sort usual for the kind of jaw possessed by the animal. In the adequately known extinct species four or five antemolar teeth are present; in *O. afer* the more anterior of these drop out as growth proceeds, but there is no reduction of the more posterior teeth. On the contrary these are similar in size to or even larger than those of the extinct species (see measurements in Colbert, 1941: 322–3). They display none of the extreme variability associated with a dentition on the decline. Their retention, together with the structure of the posterior portion of the mandible, is surely related in some way to diet.

Other than termites and ants very little in the way of animal food has been recorded. Fitzsimons mentions "locusts and other odd insects", Frassati, scarabaeid larvae, and Mitchell (1965), "beetles and other insects." Kingdon reports that "locusts are occasionally eaten", larvae are taken in quantity, "over 40 scarabaeid pupae eaten in a single night were found in one stomach," and "there is a single report of a mouse being taken." The teeth of *O. afer* are no doubt employed in the comminution of some of these, but to judge from other myrmecophagous mammals they would not be essential—the pyloric "gizzard", which is well developed (Jäger, Sonntag, Allison, 1947), could perform the task without them. Pangolins, for example, are known to eat adult beetles,[1] and captive specimens of *Manis pentadactyla* have eaten mice and young rats, which were "sucked in wholesale . . . there seemed to be no endeavour or need to chew" (Adam, 1932). Unless the aardvark's animal diet is far more varied than all reports indicate the explanation does not lie here.

The only possible clue is provided by a vegetable item in the diet. *O. afer* is known (Verheyen, 1951: 96–97; Meeuse, 1962: 62–63, 1963; Mitchell, 1965; Leakey, 1969: 113) to eat the fruit of a cucurbitaceous plant, *Cucumis humifructus* Stent, called in South Africa the "aardvark-cucumber." So close is the association between the two species that Meeuse has described it as symbiotic to some degree. The recorded distribution

[1] Pagès records them in seats of *Phataginus giganteus*, and Leakey (1969: 122) has a delightful note of a Temminck's pangolin squatting partially submerged on the shore of Lake Victoria and floating its sticky tongue out on the surface of the water to trap beetles (presumably Gyrinidae) swimming there.

of the cucurbit—South Africa, South West Africa, Rhodesia, Zambia, Tanzania and Zaire (Republic of the Congo)—coincides with that of the aardvark, and the plant is "almost exclusively found near old ant-bear holes" (Meeuse). Alone among the Cucurbitaceae, *C. humifructus* is geocarpic, the globose fruits, 5 to 9 cm in diameter, being developed at the ends of long peduncles that penetrate the ground to a depth of 30 cm or more (Meeuse). Loose soil is essential, for the peduncles, if damaged during growth, do not bear fruit; such soil is present around aardvark workings. The numerous seeds, or some of them, at any rate, pass through the animal's alimentary tract undamaged. Aardvarks bury their feces in holes about 10 cm deep, frequently in the earth excavated from their burrows, and the holes are carefully filled in (Verheyen). The seeds are thus planted in suitable soil enclosed in a packet of manure. Passage of the seeds through the animal may facilitate germination, Meeuse having noted "that it is very difficult to get seeds of *C. humifructus* to germinate in contradistinction to those of other species of the genus *Cucumis*." He goes on to state "that the aardvark is, for practical purposes, the most important if not the only dispersing agent of the seeds." So great a degree of specialization and of dependence on the part of the plant argues for a long history of its evolving association with the animal.

The advantage to the plant seems evident, but for such a relationship to come into being the benefits should be reciprocal. Since aardvarks are very partial to the fruits and actively excavate them (Verheyen) some attraction obviously exists. The pulp of the fruit "is a very juicy somewhat gelatinous soft substance with a faintly sweet cucumber taste and no appreciable flavour." For this reason Meeuse doubts that the fruit is eaten for taste or flavor if aardvark and human palates are comparable (which they may not be; for example, I do not find termites obnoxious although I would not care to subsist on them). There may perhaps be a nutritional advantage since some cucurbits are known to be rich in various vitamins, but *C. humifructus* has apparently not been investigated in this connection. Meeuse and Leakey have suggested that the fruit is a source of water. This would be decidedly beneficial even if nothing else was gained by eating it. *O. afer* has been observed to drink (Verheyen), but its range includes areas, such as the Kalahari, with prolonged dry seasons. The fruits of *C. humifructus* are protected against desiccation by a waxy covering. Such a resource would permit aardvarks to penetrate regions rich in termites that might otherwise be denied to them. Leakey's observations are to the point here: "The first seven specimens we studied [in 1945] included the seeds of a wild cucumber that grows underground. We set to work to find a reason for this. Some of our staff members located an area with several aardvark burrows and a single water hole. Each morning for a number of weeks they studied the night tracks leading to this water hole, and never saw any trace of an aardvark going to water. Apparently the aardvark often meets his needs for liquid by eating wild cucumbers."

Do aardvarks employ their cheek teeth to break up the fruit? I suspect that they do, although the only published account would suggest otherwise. Verheyen reported that one of his Congolese assistants, F. Kibwe, informed him that the fruit was broken by pressure of the muzzle and the contents licked up by the tongue ("font sauter la capsule en la pressant avec la pointe du museau, pour ensuite à l'aide de la langue, la vider complétement"). In view of the wariness of aardvarks and their nocturnal habits it seems doubtful that anyone could approach close enough to observe such fine details in the field. That a fruit with a "tough firm outer layer" (Meeuse) could be so broken also seems unlikely, particularly as the aardvark's muzzle is soft (King-

don). On the other hand the gape and the nature of the jaw articulation of *O. afer* would permit taking the fruit into the mouth, where it could be crushed with the teeth.[1] I have no other suggestion to offer, and the matter obviously requires further investigation. No one, it would seem, has presented a captive aardvark deprived of water with its "cucumber" and recorded how the animal dealt with it.

RELATIONSHIPS AND ORIGIN OF THE TUBULIDENTATA

The affinities of aardvarks have long been debated, the opinions put forward falling into three main categories: the group forms a division of an order or superorder Edentata, together with xenarthrans and pangolins; it is a very isolated order whose origin lay somewhere among the Mesozoic mammals; its relationships are with the ungulates and its ancestry was condylarthran (for the history of opinion and further references see Jepsen, 1932: 270–274; Simpson, 1945: 190, 191, 239).

Little need be said at this date regarding the first of these views, now universally abandoned. The evidence reported and reviewed above brings nothing to its support. *Plesiorycteropus* does resemble armadillos and pangolins in certain skeletal features not present in orycteropodines, but convergence, not relationship, is involved.

Broom (1909 a, b) was prominent among proponents of the second school. He saw in the primitive nature of Jacobson's organ an indication of probable marsupial affinities and of very early divergence from the eutherian stock, while in the milk dentition (interpreted by him as $di\frac{3}{3}$, $dc\frac{1}{1}$, $dm\frac{6}{6}$) "the evidence of six premolars would . . . . . suggest the possibility of its being related to some of the Mesozoic mammals, a number of which have probably an identical dental formula." It may be observed that a primitive Jacobson's organ would not be incompatible with condylarthran ancestry and that the presence of numerous tooth germs in the premolar area does not necessarily link *Orycteropus* to any Mesozoic group. A number of papers about the dentition of the aardvark and its tooth germs have been written. Despite the intrinsic interest of this subject it has nothing to do with the problem of relationships. *Leptorycteropus* reveals that a rather generalized tubulidentate had a functional canine and the normal eutherian cheek tooth number. The additional tooth germs of *Orycteropus* have no more relevance to the origin of the order than the numerous teeth of *Priodontes* have to the origin of the Edentata. Jepsen (1932), in referring *Tubulodon* from the North American early Eocene to the order, concluded that the ancestry did not lie among the Condylarthra and "must be sought in the Mesozoic." The principal evidence for his ordinal assignment of *Tubulodon* lay in the presence of tubular structures in the dentine. Discoveries made since Jepsen wrote have revealed that *Tubulodon* is a member of the palaeanodont family Epoicotheriidae (Gazin, 1952: 32–46; Simpson, 1959). Here, then, if the tubular structures are at all comparable, might be evidence in favor of the old, inclusive edentate group. However, they are surely not. Colbert (1941: 348) pointed out that they were unlike the tubules of *Orycteropus*. Gazin observed tubular structures in the teeth of the related *Pentapassalus*, but he also detected them not only in teeth but also in bones of other forms occurring in the same deposits as *Pentapassalus*. His conclusion was that they were certainly post-mortem in nature. Whatever the relationships of the palaeanodonts may be—to Xenarthra, to Pholidata or to both (Matthew, 1918: 620–657; Simpson, 1931; Emry, 1970; Patterson, 1975) they do not lie with the Tubulidentata.

[1] A comparable feat is performed by *Dasypus novemcinctus* when it takes a quail's egg into its mouth, crushes it and swallows it shell and all. Leakey has a drawing of an aardvark taking a fruit into its mouth, but whether or not this was based on observation is not stated.

The third view had a gradual growth. As comparative anatomical studies progressed during the 19th century the separation of *Orycteropus* from both manids and xenarthrans became increasingly apparent and resemblances to ungulates began to be noticed. Around the turn of the century, some authors (e.g., Smith, 1898: 387–389; Weber, 1904: 419–420) had come to believe that these resemblances indicated the real affinities, Elliott Smith apparently being the first to suggest a condylarthran ancestry. What might be called the comparative anatomical approach culminated in the work of Sonntag and others. In his summation, Sonntag (1926: 479–484) reviewed the anatomy of *O. afer* system by system, concluded that the affinities were with the ungulate orders (noting resemblances to hyracoids and proboscideans) and, drawing on the paleontological literature then available, strongly endorsed the hypothesis of condylarthran origin. Contemporaneous or subsequent work in the same vein—Woollard (1925) on the brain, Coupin (1926) on the nasal region, especially the endoturbinals,[1] Frechkop (1937) on the feet, Frick (1956) on the muscles of the head—are not in contradiction.

A minor point requires notice here. *Orycteropus* has a mesethmoid and this, according to one view, might exclude it from the ungulate assemblage entirely. Broom (1926, 1927, 1932: 317–318, 1935) split the Mammalia into two grand divisions, "Palaeotherida" and "Neotherida", the former without and the latter with an additional ossification center, the mesethmoid, in the basicranial axis. The eutherian "Palaeotherida" included Chrysochloridae (an order in his opinion), Edentata, Proboscidea, Sirenia, Perissodactyla and Artiodactyla; the "Neotherida" embraced Insectivora, Macroscelidea, Dermoptera, Chiroptera, Primates (including Tupaiidae), Rodentia, Lagomorpha, Pholidota, Carnivora, Cetacea, Hyracoidea and Tubulidentata.[1] "Most probably," he thought (1932: 318), "with the enlarging brain too much cartilage was left to be readily ossified by the presphenoid and the mesethmoid arose as a neomorph," a suggestion that took no account of the possession by various "palaeotheridans" of brains more enlarged than those of numerous "neotheridans" and ignored the likelihood that if this really was the explanation a mesethmoid might well appear independently in group after group as brain size increased. As regards distribution of the mesethmoid among the mammalian orders Broom was on shaky ground; he knew of or examined far too little material and subsequent work has proved him wrong in some instances. Among the "palaeotheridan" Artiodactyla, Starck (1967: 498–502) cites Augier's finding of additional centers of ossification in the basicranial axis of *Sus* and himself figures a clearly defined mesethmoid in a

[1] A resemblance to certain arctoids in the proliferation of the ectoturbinal system led Coupin to suggest some relationship to the Carnivora also. I believe the resemblance to be due to convergence, the arctoids in question being highly macrosmatic.

[1] Broom was a little given to this sort of thing. Earlier (1897, 1915 a and b) he had proposed two other grand divisions of the Eutheria based on the structure of Jacobson's organ. Chrysochloridae, Tupaiidae, Macroscelidea, Rodentia and Lagomorpha (probably), Edentata and Tubulidentata were included in the "Archaeorhinata"; Insectivora, Chiroptera, Primates, Carnivora, Cetacea and Sirenia (possibly), Hyracoidea, Perissodactyla, and Artiodactyla in the "Caenorhinata" (for want of material some living groups were left out of account and nothing at all was said about how an extinct order could possibly be allocated on this basis to one division or the other). Agreement between the two schemes is, not surprisingly, very far from complete. Only two "archaeorhinate" groups are also "palaeotheridan", artiodactyls and perissodactyls are "caenorhinate" but "palaeotheridan", *Orycteropus* is "archaeorhinate" but "neotheridan", and so on. That such discrepancies worried Broom is not apparent from his writings; he seems to have forgotten about "Archaeorhinata" and "Caenorhinata" by the time he proposed "Palaeotherida" and "Neotherida."

neonate *Hippopotamus* (within this order Broom studied only *Bos*, *Ovis* and *Capra*). A "palaeotheridan" order has thus been shown to include "neotheridan" members, and future findings of a similar nature may confidently be expected. Among the "palaeotheridan" Edentata, Dechaseaux (1971: 17–20) has described a median ossification in the ground sloths *Oreomylodon* and *Hapalops* that, topographically, has the attributes of a mesethmoid, and has cogently commented on the practical difficulties of determining, on the basis of basicranial ossification centers, whether extinct forms belong to one category or the other: "comment, dès lors, établir pour les Mammifères actuels et fossiles une division en *Paleotherida* et *Neotherida* qui ait une valeur assez sûre pour servir de fondement à des hypotheses d'ordre générales." As a further consideration, few would deny the "neotheridan" Hyracoidea a place among the ungulates. Jollie (1958: 274), without mentioning the mesethmoid by name, refers to it under the heading "secondary ossifications in the posterior part of the nasal capsule", i.e., structures of minor significance. I must agree with Roux (1947: 370–376), Starck, and Dechaseaux that the mesethmoid is no guide to higher groupings in the Eutheria. Possession of this bone by *Orycteropus* need not be taken into account in assessing affinities.

Until rather recently the fossil record of the Tubulidentata consisted for all practical purposes—*Plesiorycteropus* being ignored—of a few extinct species of *Orycteropus*, and paleontology was thus in no position to make any direct contribution to the problem of relationships. With the condylarth hypothesis in the air, however, paleontologists familiar with condylarthran osteology could weigh the resemblances and differences between the extinct order and the living genus across the vast intervening time gap. Thus Matthew (1937: 134–144) found the posteranial skeleton of *Orycteropus* to compare closely with that of the Paleocene periptychid *Ectoconus* and used it as the standard of comparison in his description of the latter. The resemblance, he thought, "does not involve any near relationship," a denial that no doubt stemmed from his belief (p. 196) that *Ectoconus*, as a periptychid, was a member of the now generally abandoned order Taligrada (Periptychidae and Pantolambdidae), which he regarded as broadly ancestral to most of the "subungulate" orders. He did, however, state that the tubulidentate pes was perhaps derivable from the condylarthran type (p. 319). Gregory (1910: 337) had earlier called attention to resemblances between the two groups in the astragalus, a point expanded upon by Sonntag (1926: 464–7).[1] Colbert (1941: 343–347), using the technique of deformed coordinates, carried the comparison of *Ectoconus*, which he regarded as a condylarth, further, and on the basis of the resemblances he detected concluded that the two orders ". . . . . must have had a common ancestry in basal Tertiary or late Cretaceous times. Moreover, it seems to me that this primitive ancestor probably was a condylarth." The additional evidence now available, provided by the extinct orycteropodid genera made known since Colbert wrote and by recent additions to knowledge of condylarthran osteology (*Arctocyon*, Russell, 1964: 139–189; Meniscotheriidae and Hyopsodontidae, Gazin, 1965, 1968), may briefly be reviewed.

The skulls of aardvarks and condylarths have been little compared. As far as the facial region is concerned the two groups are of course far apart, but in the cranial certain resemblances between members of the two orders are apparent. The primitive tympanic of *Orycteropus* is not fused to the skull. Its anterior crus attaches

[1] Matthew made no reference in his monograph of 1937 to this study of *Orycteropus*. The omission was no doubt due to posthumous publication, the major portion of his text having been written in 1916–1917. In 1918 (pp. 655, 656) he favored a condylarthran origin for the Tubulidentata.

to the postglenoid process and to a tubercle anteroventral to it on the squamosal-alisphenoid suture. This tubercle corresponds to the crest posterolateral to the foramen ovale described by Gazin, who suspected that it served for tympanic attachment, in *Meniscotherium* and *Hyopsodus*. The alisphenoid in orycteropodids is a major contributor to the anterior wall of the tympanic cavity, and a similar degree of participation also occurs in condylarths. The latter lack an epitympanic sinus and so does *Plesiorycteropus*. The lateral face of the periotic in *Orycteropus* is deep and nearly vertical whereas that of condylarths is less inclined, but here again *Plesiorycteropus* is closer to the condylarth condition; in neither group is the promonterium conspicuous. The paroccipital process is reduced to the vanishing point in orycteropodids; it is small in *Hyopsodus*. The alisphenoid contributes laterally to the base of the pterygoid plate in aardvarks and to a rather greater extent in condylarths. The posterior margin of the palate in *Orycteropus* is in the form of a very prominent transverse bar; a similar structure occurs in various condylarths. The lachrymal area in the two groups is similar (Gregory, 1920: 171, 176); the foramen is within the orbit in condylarths and *Plesiorycteropus*. A contact between frontal and alisphenoid occurs in *Orycteropus* and *Arctocyon*. The cranial foramina are broadly comparable in the two orders. *Orycteropus* lacks a postglenoid foramen but *Plesiorycteropus* has one. The orycteropodids do not have an alisphenoid canal but neither do all condylarths, e.g., *Hyopsodus*.

The vertebral formula in *Orycteropus afer* is C7, D13, L8, S6, Cd25. In most condylarths for which the count in whole or in part is reasonably well known—*Phenacodus*: C7, D14 or 15, L4 or 5 (not 6 or 7–Gazin), S4, Cd24; *Ectoconus*: C7, D14 ±, L4, S4; *Arctocyon*: C7, D14?, L6?—the number of lumbars is lower, but in *Meniscotherium* it is nine. The marked increase in the sizes of the posterior dorsals and lumbars over those of the anterior dorsals encountered in *Orycteropus* and *Leptorycteropus* also occur in *Meniscotherium*. The solidly built condylarthran sacrum is a structure from which the orycteropodid sacrum could readily have been derived by incorporation of anterior caudals.

Among aardvarks the scapula is known only in *Myorycteropus* and *Orycteropus*, the most fossorial members of the order. It is broad, with large pre- and postspinous fossae, coracoid process and metacromion, and an acromion that descends distally well below the glenoid cavity. No known condylarth was specialized for digging. Despite this, certain resemblances to the orycteropodid scapula occur in one member or another of the order: in *Arctocyon* the bone as a whole is rather wide, in *Ectoconus* the coracoid process is stout and recurved, as in condylarths generally (some recurvature may also occur in aardvarks) and in *Meniscotherium* a prominent metacromion is present. Various resemblances between the two orders in the structure of the humerus are apparent. The proximal end of the bone and the large deltopectoral area in orycteropodids resemble those of *Ectoconus* and *Arctocyon*, with the lesser developed area of *Leptorycteropus* finding a counterpart in *Meniscotherium chamense*. The prominent supinator crest of the orycteropodines is matched among condylarths by those of *Arctocyon* and *Ectoconus*, the lesser one of *Plesiorycteropus* by *Loxolophus* and *Meniscotherium*. Like aardvarks, various condylarths lack a supratrochlear foramen. The entepicondylar and distal articular areas are very similar in both. The radius and ulna and, in particular, the manus are specialized in tubulidentates. Neither the marked distal expansion of the radius and ulna in orycteropodines nor the distal diminution of the ulna in *Plesiorycteropus* is met with in condylarths, but the rather generalized structure of these bones in that group could have provided the base from which such

specializations arose. The aardvark manus is fully known only in *Orycteropus*. In this form the virtual elimination of the first digit, the increase in width of the rest of the foot and the concentration on the second and third digits have resulted in a widening of the lunar, a diminution of the magnum, some enlargement of the centrale portion of the scaphocentrale, a marked lateral extension of the trapezium over Mc. II (this carried even further in *Myorycteropus*), and the development of an articulation between the cuneiform and Mc. V. Most of this is on the dorsal side, however. If the manus is viewed from the ventral surface, there is, apart from the extension of the trapezium and the concomitant reduction of the trapezoid, a closer resemblance to the condylarthran carpal arrangement.

The tubulidentate pelvis is peculiar in the possession of a very prominent, laterally projecting process in the region of the ischial tuberosity. *Orycteropus* is further specialized in the extension of the ischium posterior to this process and in the dorsal expansion of the ilium above the sacral articular area. Neither character is to be seen in *Plesiorycteropus*, and the latter would appear to have been less marked in *Leptorycteropus*. Such specializations apart, there is a general resemblance between aardvark and condylarth innominates, including shape and direction of the anterior portion of the ilium, the prominent tubercle for M. rectus femoris and the spina ischiadica. The iliopectineal process, very prominent in *Orycteropus*, is much less developed in *Leptorycteropus*. The condylarth femur is rather closely comparable to that of aardvarks in overall shape, trochanters and digital fossa. The marked lateral extension of the distal end in orycteropodines does not occur in *Plesiorycteropus*. Fusion apart, tibia, and fibula are similar in the two orders as regards such features as the anteroposteriorly expanded proximal and distal ends of the fibula and the wide proximal end and prominent cnemial crest of the tibia. Tibial bowing and an interosseous crest occur in condylarths, e.g., *Meniscotherium*. Basically, the orycteropodine pes is of condylarthran type. The resemblances in the astragalus have been commented on by previous authors (that of *Plesiorycteropus* is presumably specialized). The tarsal articulations, with the exception of the calcaneonavicular facet (a specialization), agree with those seen in meniscotherids and the later phenacodontids and hyopsodontids. The long, transversely compressed tubulidentate entocuneiform is approached in members of these families. In *O. afer* the wedge-shaped ectocuneiform thrusts up between cuboid and navicular, imparting a somewhat alternating appearance to the tarsus in dorsal view. *O. gaudryi*, in which the wedge shape of this bone is less accentuated and the narrower cuboid has a less outwardly and downwardly sloping medial articular surface, suggests that the condition in the surviving species is secondary, related to the widening of the pes within the *Orycteropus* lineage. The relations of the metatarsals to the distal tarsal row and to each other, including the proximal overlap of the dorsal portion of Mt. III over Mt. IV, are again as in the three families mentioned above.

All in all, there is a strong similarity between condylarths and aardvarks in the skeleton, with many of the features seen in the latter either actually occurring in one or more of the families of the former or capable of derivation from a condylarthran base. Available data are consistent with the hypothesis that the one order was derived from the other.

Evidence bearing on the place of origin of the Tubulidentata is indirect yet suggestive. The earliest members of the order so far known occur in Africa. Two extinct lineages of the Orycteropodinae were present there. The divergently specialized *Plesiorycteropus*, whose ancestors reached Madagascar from Africa probably at some

time in the Eocene, further tilts the scales. The only evidence that might argue against an African origin is provided by two bones from the Phosphorites, both a little damaged, described by Filhol (1894: 135–6, 140–1). One of these, a humerus, he referred to the Orycteropodidae as *Palaeorycteropus quercyi*. The other, a tibia, which he compared with that of the pangolins, was later made the type of *Archaeorycteropus gallicus* by Ameghino (1905: 223).[1] Neither is convincingly orycteropodid-like. Simpson (1931: 374) considered both to be indeterminate, and Thenius (1960: 196n) concluded that *Palaeorycteropus* " . . . gehört sicher nicht zu den Tubulidentaten." Both, I think, should be listed as Eutheria *inc. sed.*[2]

In agreement with such authors as Lavocat, Arambourg, and Cooke, I believe on present evidence that the Tubulidentata came into existence in Africa, possibly in Paleocene time, one of a number of groups that arose there during the isolation of that continent during the earlier Tertiary. What the relationships of the order may have been to the other distinctively African ungulate groups, all presumably of condylarthran ancestry, is at present quite uncertain. For evidence bearing on this and on numerous other problems concerning the early history of mammals in Africa we must wait upon future discoveries.

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[1] In the same paper he referred a broken distal end of a tibia (now lost) from the early Eocene Casamayor Formation of Patagonia to this "genus", as *A. patagonicus*. Simpson (1948: 94) very justifiably regarded the "species" as a *nomen vanum*.

[2] A third Phosphorites form sometimes mentioned in this connection is *Leptomanis quercyi* Filhol 1894, based on an incomplete dorsal portion of a skull. Filhol believed the specimen to represent a manid showing points of resemblance to myrmecophagids, Simpson regarded it as "indeterminate, possibly an orycteropodid", and Emry, with whom I agree, would include it in the Manidae "with the understanding that its real identity may not be known."

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AN ECOLOGICAL AND SYSTEMATIC SURVEY OF FISHES IN THE RAPIDS OF THE LOWER ZAÏRE OR CONGO RIVER

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Abstract. Rapids habitats at nine localities along the mainstream of the Zaire River between Kinshasa and Matadi were fished extensively with rotenone during low water, yielding over 7000 specimens belonging to 129 species. A total of 17 families are represented, the most speciose being Mormyridae (19 species), Cyprinidae (19), Cichlidae (17), and Mochokidae (16). Limnological and ecological observations are reported for the rapids habitats, and the adaptations and mode of reproduction of the fishes discussed.

Nineteen new species are described from the Lower Zaire rapids, belonging to the genera *Mormyrus, Alestes, Labeo, Bagrus, Chrysichthys, Notoglanidium, Gymnallabes, Chiloglanis, Lamprologus, Nanochromis, Steatocranus, Teleogramma,* and *Mastacembelus,* most of them with obvious modifications for life in the rapids. *Caecomastacembelus* is placed in the synonymy of *Mastacembelus,* and morphologically intermediate hybrids reported between blind, depigmented *Mastacembelus brichardi* and normally eyed, darkly pigmented *Mastacembelus brachyrhinus.* The genera *Campylomormyrus* (elephant-snouted mormyrids), *Steatocranus* and *Teleogramma* are fully revised. Of 16 nominal species of *Campylomormyrus,* only three are regarded as biologically valid. In addition to one new *Steatocranus* from the mainstream of the Lower Zaire River, two new species of this rheophilic cichlid genus are described from elsewhere in the Zaire basin, making a total of 21 new fishes described in this paper. *Leptotilapia* is placed in the synonymy of *Steatocranus,* which now comprises eight species. *Bryconaethiops yseuxi* is shown to be a valid species, and data on the number of mandibular tooth families are used to distinguish the closely related *Atopochilus guentheri* and *A. royauxi.*

Two ecological categories of highly specialized rapids fishes are recognized: strongly rheophilic or current-loving, comprising 58 of the species in our survey, and hyporheic or intrusive, comprising eight species which evidently avoid light as well as strong current by delving deeply into the interstices offered by jumbled piles of rocks, and perhaps, in some cases, burrowing into mud or loose rubble. The most consistent evolutionary modification of the rapids fishes is reduction (but not complete loss) of the eyes. Of 66 highly specialized rapids fishes, 26 are microphthalmic (with small or minute eyes superficial in position), five cryptophthalmic (eyes reduced in size and partially or completely covered over by skin and

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other tissues), and only one is anophthalmic (totally without eyes). The most startling discovery of the survey is a cryptophthalmic cichlid of the genus *Lamprologus*. This is the first reported blind species of percoid fishes.

Some relationships between the rapids fishes and the ichthyofauna of the Zaire basin and of Africa as a whole are pointed out in the discussion. The opportunities for speciation and adaptation provided by rapids habitats have contributed significantly to the diversity of the highly endemic ichthyofauna of the Zaire basin, a process much less noticeable elsewhere in Africa, where highly specialized rapids fishes are relatively few. A few rheophilic genera, namely *Campylomormyrus, Atopochilus,* and *Steatocranus,* presumably evolved in the Zaire basin, subsequently spreading to one or more river systems in the adjacent Lower Guinean and Nilo-Sudanic ichthyofaunal provinces. The great majority of species of rapids fishes in the Zaire basin are endemic, many of them apparently restricted to the 300-km stretch of the Lower Zaire River between Kinshasa and Matadi. Most of the rapids genera, however, are widely (if discontinuously) distributed in the Zaire basin, wherever suitable habitat occurs. Perhaps the most striking aspect of the taxonomic composition of the Zairean rapids fishes is the preponderance of Cichlidae, which contributed more than a third of the endemic rapids species and also more than a third of the total number of individual specimens taken during our rapids survey. Such predominance of Cichlidae is a noteworthy contrast to the situation in rich riverine faunas everywhere else in Africa, including low gradient rivers in the Zaire basin, where cichlid species, endemic or not, are always few in number and seldom contribute substantially to the numbers of individuals present. Evolution in rocky rapids habitats may well have contributed to preadapt Zairean cichlids, including *Lamprologus,* to explosive lacustrine evolution along the rocky shores of Lake Tanganyika.

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For consulting with us on the rapids fishes and for helping with the identification of a number of species we found particularly troublesome, we are indebted to our friend and colleague, Prof. Max Poll, who has been studying and publishing on the fishes of Zaire steadily since 1932. Mr. Gordon Howes responded with his characteristic promptness and thoroughness to our requests for information about types and other specimens housed in the British Museum. Drs. Ruth Turner and John Lawrence, of the Museum of Comparative Zoology, kindly identified mollusks and insects recovered from the guts of our fish specimens. The photographs of fishes were prepared by Mr. Alphonse Coleman and Miss Paula Chandoha in the photographic lab of the Museum of Comparative Zoology, and were paid for by a grant from the Milton Fund of Harvard University. Publication was assisted by a grant from the Wetmore Colles Fund.

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INTRODUCTION

The Zaire or Congo basin, with an area of 3,822,000 km, lies at the heart of Africa.

About 37% of its catchment is in the northern hemisphere and 63% in the southern. The Upper Zaire River or Lualaba arises in Zambia and flows northward to Kisangani; its catchment lies south of the Equator and includes lakes Bangweulu, Moero, Kivu, and Tanganyika. The Middle Zaire River flows westward in a great arc from Kisangani to Kinshasa. Its catchment comprises all of the Zaire basin north of the Equator and roughly two-thirds of that to the south, and includes the entire Cuvette Centrale. The largest tributaries in the Zaire basin, the Ubangui (also spelled Oubangui, Ubanghi, and Ubangi) in the north and the Kasai in the south, are received by the Middle Zaire River. The Lower Zaire River extends from the outlet of Malebo Pool to the sea. Its catchment extends from 3 to 6° south and comprises only 2% of the total area of the Zaire basin. The largest tributaries of the Lower Zaire River—the Inkisi, Kwilu, and Mpozo—are insignificant compared to the Ubangui and Kasai.

The Upper Zaire River and its tributaries are beset by numerous rapids, including those at the Portes d'Enfer, near where the Lualaba receives the Luvua, and the Stanley Falls, a series of falls and rapids in the last 150 km of the Lualaba immediately upstream from Kisangani. Major rapids occur in the Ubangui and Kasai rivers and in the upper portions of most important tributaries to the Middle Zaire River. (In contrast, the mainstream of the Middle Zaire River and some of its tributaries that arise entirely within the Cuvette Centrale are devoid of rapids; the slope of the Middle Zaire River never exceeds 8 cm per km). Almost all tributaries of the Lower Zaire River are high gradient streams with numerous rapids. Some of the tributaries, such as the Inkisi, have major falls where they enter the mainstream of the Zaire River.

At Kinshasa, having flowed all but 450 of its 4,650 km length, the Zaire River encounters a barrier formed by a rocky sill and expands into Malebo Pool. For the next 300 km, as the river flows over the sill and on through a gorge in the Crystal Mountains, it is broken by numerous cataracts, with intermittent stretches of calm water. The last of the rapids, just upstream from Matadi, are about 130 km from the sea. Between Kinshasa and Matadi the river drops 270 m; the average slope of this portion is therefore 90 cm per km. Recent collections in rapids habitats near the fishing village of Kinsuka, a few km downstream from Kinshasa, resulted in the discovery of several highly specialized fishes, including an extraordinarily flattened, microphthalmic clariid catfish and a cryptophthalmic mastacembelid eel (Poll, 1959, 1966, 1973; Roberts, 1968).

In 1973, with a grant from the National Geographic Society, we made ecological observations and collections of fishes at previously unsampled rapids localities between Kinshasa and Matadi. Most of the rapids fishes hitherto known only from Kinsuka were found further downstream. Nineteen new species were discovered, including several microphthalmic catfishes, three more strange mastacembelids, and the first known blind cichlid. The descriptions of these new species and identifications of all other species taken at the mainstream rapids localities where we were able to collect are presented in this paper. In connection with this work we have revised the mormyrid genus *Campylomormyrus* and the cichlid genera *Nanochromis sensu stricto, Steatocranus* and *Teleogramma*. Three new rapids-inhabiting *Steatocranus* are described, one from the mainstream of the Lower Zaire River, one from the Mpozo, and one from a tributary of the Ubangui River. All other new species described in this paper are from mainstream rapids in the Lower Zaire River.

Poll (1959) reported a total of 117 fish species from Malebo Pool, all of which are now known to be widely distributed in the Zaire River. Our survey brings the total number of species collected in or near rapids habitats along the mainstream of the

Lower Zaire River to 147. Of these, 34 are unknown elsewhere and are presumably endemic to this section of the river. The Zaire basin is thought to have been an interior drainage through the Miocene and most of the Pliocene, perhaps forming an immense lake or a series of lakes in the Cuvette Centrale. According to this theory, Malebo Pool lies at the western end of the former drainage, which was captured in the late Pliocene or early Pleistocene by a Lower Guinean coastal river (Cahen, 1954; Howell and Bourlière, 1963; Roberts, in press). If this interpretation is correct, the endemic fishes in the Lower Zaire rapids must have evolved subsequently, since before then the rapids habitats would have been too small and unstable, and the coastal stream would have been inhabited by a Lower Guinean ichthyofauna, lacking in many of the characteristic Zairean genera which have given rise to the endemic rapids species. The zoogeographic relationships among the fish faunas of Lower Guinea, Angola, and the Zaire basin are discussed by Roberts (in press).

LIMNOLOGY

An introductory account of the limnology of the Zaire basin is given by Marlier (1973). At Malebo Pool the discharge of the Zaire River fluctuates from 23,000 to 50,000 cubic meters per second. This relatively stable flow of the Lower Zaire River is mainly attributable to the humidifying and spongelike properties of the forests which cover much of the Zaire basin and to the seasonally alternating contributions of the huge northern and southern tributaries of the Middle Zaire River. The high water level in the Zaire mainstream is seldom more than 3 m above the low water level. The amplitude of the annual fluctuation is 2.38 m in the upper Lualaba, 2.68 m at Kisangani, 1.81 m at Mbandaka, rises to 3.5 m in the "channel" or narrow section immediately upstream from Malebo Pool, and falls to a little over 2 m in Malebo Pool (Marlier, 1973:226). At certain places where the gorge of the Lower Zaire River narrows to several hundred meters the amplitude may greatly exceed 3.5 m. Bequaert and Clench (1936: 161) reported a difference of from six to eight meters at Matadi. Concerning the rise and fall of water level at the beginning of the rapids, Poll (1959:91) quoted Pierre Brichard to the effect that the water rises from at least two meters at the northern end of the île des Mimosas to more than ten meters at the southern end of the île du telephone. The île du telephone is a large island about 3 km below the beginning of the rapids, which divides the mainstream into two narrow channels; the île des Mimosas is not named on our maps, but is presumably the small island at the very beginning of the rapids, connected to the mainland by a cement causeway. (Brichard is the aquarium fish collector who originally discovered the blind mastacembelid and other rapids fishes described by Poll.) On the steep walls of the gorge near Wombe, we observed high water marks fully ten meters above the level at the time of our visit (Plate 1, a).

Temperature, dissolved O_2, pH and alkalinity were routinely taken at our collecting stations; data for the mainstream of the Lower Zaire River between Kinshasa and Matadi and its northern and southern tributaries are recorded in Table 1. At all mainstream localities the water temperature was higher than in the tributaries, dissolved O_2 was high, pH near neutral, and alkalinity extremely low. Phenolthalein alkalinity was always zero. The relatively high pH and alkalinity of the southern tributaries is attributable to the limestone formations in which they originate. Our O_2, pH and alkalinity measurements were made with a water analysis kit manufactured by Hach Chemical Co., Ames, Iowa (model AL–36B). Proceeding downstream from Gombe to Inga we encountered a progressive lowering of mainstream water temperatures from 29°C to 24.7°C. Perhaps the main factors which contributed to this

Table 1. Temperatures and water chemistry for northern and southern tributaries and mainstream of Zaire River between Kinshasa and Matadi, 23 June–1 September 1973.

Localities (n)	Temperatures °C		Dissolved O_2 (mg/l)	pH	Alkalinity[1]
	Water	Air			
Northern tributaries (11)	19.0–23.9	21.5–28.8	8.0–9.0	7.0–8.5	1–12
Southern tributaries (13)	21.0–24.5	22.0–31.0	7.0–9.0	6.5–9.0	1–14
Mainstream (7)	24.7–29.0	23.3–30.0	8.0	7.0–7.5	2–3

[1] Total (Methyl Orange) alkalinity in grains/gal $CaCO_3$.

drop of 4.3°C in 270 km are 1.) evaporative cooling enhanced by turbulence; and 2.) input of tributary water averaging about 5°C cooler than that of the mainstream. If this explanation is correct, the downstream cooling could be a year-round phenomenon.

Light penetration in the Lower Zaire River is generally poor due to turbidity and to humic coloring substances arising in the Cuvette Centrale. Visibility of less than 10 cm was encountered at a depth of 3 m in a gently circulating backwater near Tadi. Even in still waters from which the suspended material had settled visibility was usually less than one meter. Roberts (1968:127) observed dense growths of plants resembling eel-grass and sea-lettuce on rocks in side channels of the rapids near Kinsuka, and we noted their continued presence during a brief visit to the same area in 1973. Such a concentration of aquatic macrophytes in the rapids of the Lower Zaire River is atypical. We saw virtually no higher aquatic plants in mainstream rapids habitats further downstream except dead or dying water hyacinth (*Eichhornia*), all or most of which had originated upstream. Plant growth seemed to be restricted to rocks just below the surface of the water. The luxuriance of macrophytes in the side channels of the rapids near Kinsuka is perhaps related to the relatively clear waters flowing from Malebo Pool, and the low amplitude of water level fluctuation in these particular channels. Even more important may be nutrients arising from Kinshasa. Our overall impression of the Lower Zaire River between Kinshasa and Matadi is one of low productivity. Crocodiles and hippopotamus, which might contribute to nutrient cycling, appear to be rare. We saw no crocodiles or crocodile tracks along the mainstream, nor did we hear reports of crocodile attacks on man. We saw the tracks of only one hippopotamus, at Isangila.

Three forms of encrusting sponges, the shrimp *Atya gabonensis* Giebel, insects, and a number of molluscs were the only aquatic macroinvertebrates encountered in the field. Stomachs of a few fishes from the rapids were later found to include potamonid crabs. Almost all of the mollusks encountered in rapids habitats in the Lower Zaire River are specialized for attachment to rocks. The following gastropods, identified by Dr. Ruth Turner, were found in the guts of fishes collected in the rapids:

Ampulariidae
  Pila leopoldvilliensis Putzeys
Bulimidae
  Bulimus (*Parabithynia*)
Assimineidae
  Septariellina congolensis Bequaert and Clench
Melaniidae
  Cleopatra broecki Putzeys
  Cleopatra hargeri Smith
  Cleopatra cf. *langi* Pilsbry and Clench
  Potadoma wansoni Bequaert and Clench.

Steatocranus gibbiceps, the most abundant fish species in our rapids collections, is apparently specialized for feeding on gastropods, which it ingests whole and without crushing; *Septariellina congolensis*

TABLE 2. NUMBERS OF SPECIES AND OF SPECIMENS OF FISHES TAKEN AT NINE COLLECTING LOCALITIES IN THE RAPIDS OF THE LOWER ZAIRE RIVER.

R & S locality no.	2	19	29	35	28	26	57	38	41
Species	64	44	49	57	55	27	21	63	71
Specimens	630	215	943	1505	961	118	112	1611	1054

has been identified in its gut contents. An account of the rheophilic mollusks in the Lower Zaire River is given by Bequaert and Clench (1936; 1941).

COLLECTING METHODS AND LOCALITIES

Fishes were collected from rapids habitats at nine localities along the mainstream of the Lower Zaire River (Figure 1) from late June through mid-August, 1973, during the period of low water. (Throughout this paper, these localities will be considered in the same sequence, proceeding downstream from Kinshasa.) The numbers of species and of specimens taken at each locality are indicated in Table 2. The great majority of specimens were obtained using rotenone and dip-nets, usually with the aid of several locally recruited helpers. Dip-nets were made of woven-meshed, plastic fly-screen. At most localities the collection is a composite of two or more samples taken with rotenone. In a few instances additional specimens were obtained by other methods.

R & S 2. Near Gombe (or Ngombe), about 20 km downstream from Kinshasa. Lat. 4°24′S, Long. 15°10.5′E. Water 29.0°C. 23–25 June.

Shoreline and river bed exposed by low water; huge boulders 1–3 m in diameter interspersed with fine sand. Two rotenone samples were made among boulders along the edge of the mainstream, in strong current where recovery of fishes was only fair. Two additional samples were made, one in a broad, shallow stream, less than a meter deep, with swiftly flowing water over a rock rubble bottom, the other in a side channel 1–1.5 m deep, with a strong, surging current and jumbled rock bottom. A few specimens were seined from relatively calm water on a sandy beach where a small tributary entered the mainstream. Our first specimens of *Teleogramma depressum* and *Mastacembelus brichardi* came from this locality.

R & S 19 (*Plate 1, a*). Near Wombe, about 10 km N of Gombe-Matadi and 1 km downstream from mouth of rivière Luasi. Lat. 4°54′S, Long. 14°42′E. Water 28.5°C. 5 July.

Gorge with steep, deep sides. Edges of mainstream with large piles of huge boulders, high sand beaches. Some previous high water marks on emergent rock piles and on the walls of the gorge were as much as 10 m above water level on the day of our collecting, but what appeared to be the most recent high water mark was only 3 or 4 m higher. Two rotenone samples were taken among huge boulders at the outer edge of an extensive rock pile jutting into the mainstream. Recovery of fishes was poor because of the strong current and marked surge.

R & S 29 (*Plate 1, b*). Near Bulu, about 15 km downstream from Luozi. Lat. 5°1′S, Long. 14°1′E. Water 26.7°C. 15 July and 18–19 August.

On July 15 a large rotenone sample was taken in a pool with rock sides 2–3 m high or more, in a water depth to 1.5 m over a bottom of extremely irregular, continuous rock rubble. The pool was at the narrow end of a long cove which had a gently surging current rising and falling 15–20 cm every five or ten minutes. With a half dozen volunteers from Bulu we succeeded in capturing almost all of the fishes which appeared at the surface during the sam-

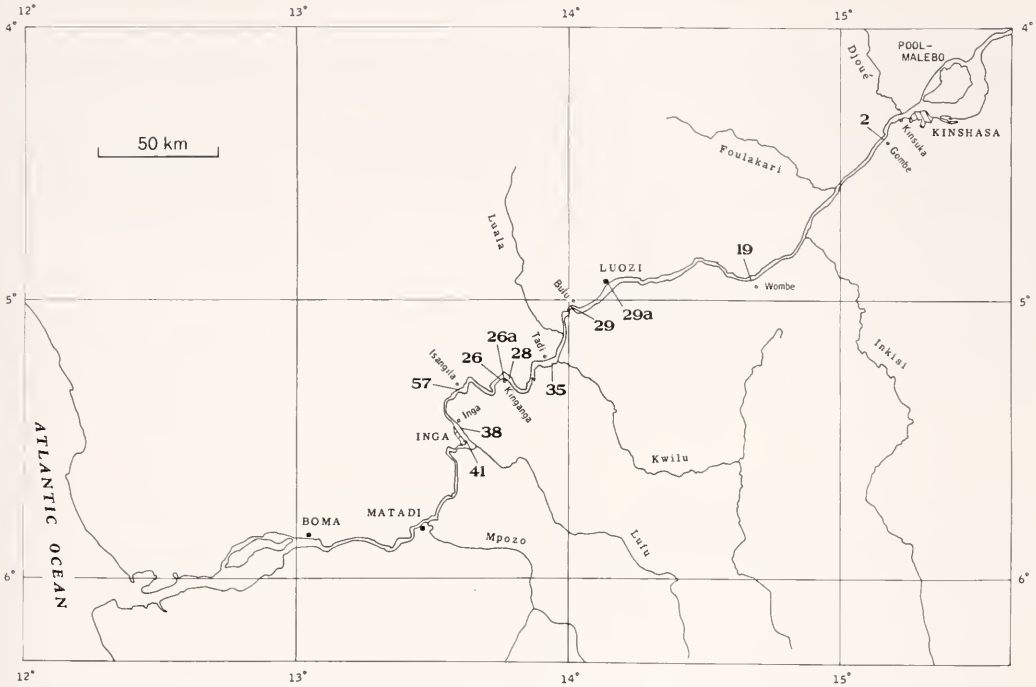

Figure 1. Map of Lower Zaire River, showing principal localities discussed in this paper.

pling. This pool yielded our one large series of *Mastacembelus crassus* and our only *Lamprologus lethops* and *Mastacembelus latens*. Two additional small rotenone samples were made, one on the edge of the mainstream current on the outside of the long cove, the other along a steeply shelving shore with hugh boulders and relatively calm water at the time of our collecting; recovery in both of these sites was poor. A few specimens were taken by seining on a sandy beach.

On August 18, a few days after the river had started to rise, this locality was revisited in an attempt to get another good rotenone sample and additional specimens of *Lamprologus lethops*. A sample was taken in the wide end of the long cove that had been partially sampled on July 15, but with poor results. The bottom at this end of the cove was mainly sand and mud, with only a few scattered rocks; water depth to 2 m. A second sample, taken about a kilometer downstream in a rocky cove broadly open to the strong mainstream current, was also poor because of the rising water. Returning to the long cove, a number of dead fishes were along the edge of the narrow end of the pool where the first *Lamprologus lethops* had been taken, and among them a dry and nearly complete specimen of this blind cichlid. A large number of clupeids and a few characins were taken in open water by fishing from a canoe at night with a large local dip-net used for fishing clupeids.

R & S 35 (*Plate 1, c*). Near Tadi, about 50 km downstream from Luozi. Lat. 5°14′S, Long. 13°56′E. Water 24.9°C. 21–22 July.

Long rocky points alternating with sandy embayments, because of vertically tipping sedimentary strata lying perpendicular to the river bed. One rotenone sample was made in a pool 1.5 m deep, with a bottom of rock rubble and sandy patches, which had become isolated from the mainstream not long before our visit. Fish were abundant and recovery good. Another rotenone

sample was made in the narrow entrance to a long lagoon (Plate 1, c), where the water surged strongly over a rocky sill, in water .5 to 2 m deep. A dozen volunteers helped pick up fishes, and recovery was good. This sample site yielded our large series of *Notoglanidium pallidum*. A few large specimens of some of the commonest species were not preserved. A third rotenone sample was taken in a backwater up to 2 m deep with boulders 1–2 m in diameter and a silty or sandy bottom. Few fishes were present in this backwater, which yielded our only specimen of the completely eyeless clariid *Gymnallabes nops*.

R & S 28 (Plate 1, d). About 4–5 km upstream from Kinganga. Lat. 5°16′S, Long. 13°47′E. Water 27.4°C. 12 July.

At this locality we found an island perhaps 2 km long, 100–200 m wide, with a shallow valley running its full length and rocky sides rising to 20 m. An intermittent series of large pools, some of them largely dry, extended the length of the valley. A rise in water level of two or three meters would presumably cause a raging torrent to pass through this valley. A large rotenone sample was taken in a pool at the lower end of the island. The pool, about 50 m long and 30 m wide, was up to 1.8 m deep but mostly shallower, with an extremely irregular bottom of rock rubble. Water was gently flowing out of the pool through a much constricted, shallow connection to the mainstream, but otherwise the water in the pool appeared to be still. Recovery of fishes was only fair, because of the extremely rough bottom, and the presence of electric catfishes which had not entirely succumbed. A few large fishes were not preserved, including a 550-mm specimen of *Lates niloticus*, the only one that we saw in the rapids. Pick-up was curtailed by nightfall. One other rotenone sample was taken, in a small area on the edge of the mainstream on the outer side of the island (Plate 1, d). A strong current flowed through vertically tipped sedimentary rocks with knifelike edges in strata parallel to the current; depth .5–1 m. Recovery fair. Our first specimens of *Mormyrus iriodes* were obtained from fishermen near the island.

R & S 26. A few kilometers downstream from Kinganga, below the mouth of the rivière Grande-Pukusi. Lat. 5°20′S, Long. 13°43′E. Water 27.4°C. 11 July.

Two parallel points of obliquely tipping sedimentary strata, 7–10 m wide, extended about 50 m into the mainstream. A single rotenone sample was taken between the points, in water up to 2 m deep over a predominantly silty sand bottom. Fishes were small and few in number; recovery fair. The sample included three of our four specimens of the tiny cichlid *Nanochromis minor*.

R & S 57. Near Isangila. Lat. 5°18′S, Long. 13°36′E. Mainstream water temperature not recorded. 15 August.

The river bed near Isangila is very broad; low water exposed extensive rock piles, cobblestones, and sandy beaches. Less than a kilometer downstream from Isangila, a small tributary flowed into a braided channel, forming pools with rocky and sandy bottoms. Water flowing into these pools from the tributary was 20.5°C. At high water the pools would be covered by the mainstream. A rotenone sample was made in a pool 20 m in diameter and up to 2 m deep, and in the shallow braided channel which constituted its outlet and flowed into the mainstream about 200 m away. Rel-

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Plate 1

Zaire River between Kinshasa and Matadi at low water (late June through early August, 1973), looking downstream.

a. At Wombe. Excellent view of gorge. At high water river rises above rocks at center of picture and covers dark areas on base of cliffs. Collections were made at outer edge of rock-pile jutting into river (R & S 19). 23 June.

Plate 1

b. At Bulu. Mainstream to the left. About three or four weeks before river started to rise. A large collection was made at narrow end of large pool near center of picture (R & S 29). This pool is the type locality of *Notoglanidium pallidum*, *Lamprologus lethops*, *Mastacembelus crassus*, and *Mastacembelus latens*. 15 July.
c. Opposite Tadi. Near type locality of *Chrysichthys helicophagus* and *Gymnnalbes nops* (R & S 35). 21 July.
d. About 5 km upstream from Kinganga (R & S 28). 12 July.
e. A few kilometers upstream from Inga hydroelectric installation, on opposite side of river. Near type locality of *Chiloglanis carnosus*, *Nanochromis parilus*, *Nanochromis splendens*, and *Teleogramma depressum* (R & S 38). 1 August.
f. About a kilometer directly West of Inga hydroelectric installation. Portion of long channel from which bulk of specimens at R & S 41 were collected. This channel is the type locality of *Mormyrus cyaneus*, *Mormyrus iriodes*, *Labeo lividus*, *Bagrus caeruleus*, and *Mastacembelus aviceps*. 4 August.

atively few kinds of fishes were present; recovery fair.

A few kilometers downstream the river narrows considerably. At this point we found rocky promontories jutting well into the mainstream, with a series of high isolated pools, up to at least 5 m above the river level, which was near its lowest at this time. A rotenone sample was made in one large pool, which must have formed part of the mainstream rapids at high water, but it did not have any specialized rapids fishes. Recovery was good; pick-up was curtailed by nightfall, and some larger fishes were not preserved.

R & S 38 (*Plate 1, e*). Near village of Inga, a few kilometers upstream and on the opposite side of the river from Inga hydroelectric dam. Lat. 5°27.5′S, Long. 13°36′E. Water 24.7°C. 1 August.

A continuous rapids 10–12 km long commences near the village of Inga. This is probably the most extensive rapids in the Lower Zaire River. A large rotenone sample was made in a long, narrow side channel, .5 to 2 m deep, with a strong current. At the upper 20 m of the channel, separated from the mainstream only by a wall of rock, the channel was only 1–3 m wide, with a rocky bottom. Before re-entering the mainstream it expanded into a lagoon about 40 m wide and 2 m deep with sand and rock bottom. Fishes were abundant; recovery good. This site yielded our first specimens of *Mastacembelus aviceps*. Another sample was taken in a small, surging backwater open at its upper end to the strong mainstream current. The backwater had high rock walls, and except at very low water it must be covered by a terrific current. The backwater was 20 m long and 1 m deep, with an extremely rocky bottom. Fishes were abundant; recovery good. Large numbers of *Mormyrops engystoma*, *Stomatorhinus* sp. or spp., and *Steatocranus tinanti* were collected. A third rotenone sample was made in a pool about 100 m from the mainstream and connected to it by a narrow channel, with water slowly surging in and out; depth .5 to 1.5 m, bottom rocky with patches of sand. Fishes were small but numerous; recovery good.

R & S 41 (*Plate 1, f*). Near Inga hydroelectric dam. Lat. 5°31.5′S, Long. 13°37.5′E. Water 24.8°C. 4–6 August.

At the dam site a 50 m head of water is obtained for hydroelectric power in about 8 km indicating a drop of about 6 meters per kilometer. At high water the river is three or four kilometers wide, but at low water it is confined to a channel less than a kilometer wide. The low water channel is narrowest where it passes to the left bank of the "coude de Inga", where the main course of the river suddenly makes a 120° turn from southeast to due west. The resulting cataracts are awesome, leaping, and throwing spray high into the air. On the right bank of the coude, low water exposes a huge area of rocky river bed two or three kilometers wide, laced with a number of channels with flowing water.

A very large rotenone sample was taken from about one kilometer of a long channel, with moderate current, numerous pools, and a predominantly rocky bottom. The place where rotenone was initially applied is shown in Plate 1, f. At one point the channel flowed strongly for several meters underneath huge boulders; almost all of the *Mormyrus* and *Rheoglanis* taken at this locality came from under these boulders. Some fishes were so abundant that all of them could not be preserved, including two or three hundred *Gymnallabes tihoni*, and were distributed among the half-dozen volunteers assisting us. A few small rotenone samples were made in shorter stretches of nearby channels with sandier bottoms; these comprised relatively few specimens and did not include any additional species. Three discrete small rotenone samples were taken, all from small, isolated, rocky pools near the mainstream, with sandy bottoms, one a few kilometers upstream from our main sampling site, the other two several kilometers downstream. These small samples, which were combined

in the field, include our only specimens of *Nanochromis consortus* and *Steatocranus glaber*. Our only Lower Zaire specimen of *Alestes comptus* was recognized in the field and came from the upstream sample.

TABULATION OF SPECIES COLLECTED FROM RAPIDS IN THE LOWER ZAIRE RIVER

In Table 3 are listed all species, and almost all specimens, of fishes collected by us in or near rapids habitats along the mainstream of the Lower Zaire River. The only other specimens obtained from the Lower Zaire River between Kinshasa and Matadi were a few large Mormyridae and *Synodontis* purchased from fishermen at Luozi (R & S 29a, MCZ 50566–50572), and some small fishes, mostly Clupeidae and Cyprinidae, captured at night near Kinganga (R & S 26a, MCZ 50573–50581).

Disposition of specimens. All of the specimens in Table 3 were initially catalogued into the fish collection of the Museum of Comparative Zoology as MCZ 50100–50565, except the holotype of *Bagrus caeruleus*, which was subsequently given MCZ 50582. A few specimens, all or almost all from large lots, were used for alizarin preparations; these retain the original MCZ catalog numbers. Paratypes of most of the new species have been sent to the Musée Royale de l'Afrique Centrale (Tervuren), British Museum (Natural History), and Smithsonian Institution.

A representative series from the collection has been designated for the Republique of Zaire, and the Directeur-general of the Office National de la Recherche et du Développment in Kinshasa has been so informed.

SYSTEMATICS

The authorities as well as the identifications of all species encountered during our mainstream rapids survey are cited in Table 3. In the present section we describe 19 new species from the Lower Zaire rapids, belonging to the genera *Mormyrus, Alestes, Labeo, Bagrus, Chrysichthys, Notoglanidium, Gymnallabes, Chiloglanis, Lamprologus, Nanochromis, Steatocranus, Teleogramma,* and *Mastacembelus*. The genera *Campylomormyrus, Nanochromis sensu stricto, Steatocranus,* and *Teleogramma* are fully revised, and two additional new species of *Steatocranus* described, one from the rivière Mpozo in Lower Zaire, the other from the rivière Mbomou in Ubangui. A lectotype is designated for *Nanochromis nudiceps*.

Caecomastacembelus is placed in the synonymy of *Mastacembelus*; intergrades, tentatively interpreted as interspecific hybrids, are reported between the cryptophthalmic, depigmented *Mastacembelus brichardi* and *Mastacembelus brachyrhinus*, its microphthalmic and darkly pigmented close relative. Systematic observations are also presented for the genera *Bryconaethiops* and *Atopochilus*. The rheophilic species *B. yseuxi*, hitherto placed in the synonymy of *B. microstoma*, is shown to be valid. Data are presented on the number of mandibular tooth families in *A. guentheri* and *royauxi*, a character which can be used to distinguish these closely similar species at all sizes.

Of the as yet unresolved systematic problems posed by our rapids material, two may be commented upon. A new *Amphilius* is to be described by Prof. Max Poll, to whom our material has been sent for study. Perhaps the outstanding problem is that represented by *Stomatorhinus*, of which a dozen species have been named, with little consideration for possible intraspecific variation. At several rapids localities we found two or three phena, but the distinctions between them were sometimes blurred by variability. We found it especially difficult to sort out the numerous juveniles obtained. In short, we feel that *Stomatorhinus* should be revised before any specimens are identified or additional new species described, and that the revision must be based on a good geographical representa-

TABLE 3. NUMBER OF SPECIMENS AND STANDARD LENGTH TO NEAREST MM OF ALL SPECIES OBTAINED AT NINE COLLECTING LOCALITIES ON THE LOWER ZAIRE RIVER. Species printed in boldface are dealt with in the systematics section of this paper. These specimens have received catalog numbers MCZ 50100–50565, 50582 in the fish collection of the Museum of Comparative Zoology, excepting the 550-mm *Lates niloticus* from R & S 28, which was not preserved.

	R & S 2	R & S 19	R & S 29	R & S 35	R & S 28	R & S 26	R & S 57	R & S 38	R & S 41
POLYPTERIDAE									
Polypterus ornatipinnis Boul. 1902	2:68–109				3:84–178			1:367	
CLUPEIDAE									
Microthrissa minuta Poll 1974			3:44–45	3:13–43	7:15–24		1:37		
Nannothrissa parva (Regan) 1917						1:21			
Odaxothrissa vittata Regan 1917	1:65		4:50–64		116:28–79	2:33–34	59:30–67		6:40–67
Poecilothrissa congica Regan 1917	1:38	1:41	73:45–54				6:28–55		8:30–50
Potamothrissa acutirostris (Boul.) 1909	1:29		2:63						
Potamothrissa obtusirostris Boul. 1909			59:56–65						3:37–57
MORMYRIDAE									
Campylomormyrus mirus (Boul.) 1898		1:104							
Campylomormyrus rhynchophorus (Boul.) 1898	6:48–113	11:29–135	3:105–169	1:365			1:105	5:55–86	21:41–99
Hippopotamyrus psittacus (Boul.) 1897		1:63							
Hippopotamyrus macrops (Boul.) 1909					1:170			1:71	
Marcusenius monteiri (Günther) 1873			2:82–101				10:100–114		
Mormyrops deliciosus (Leach) 1818	29:33–172	4:45–77	1:69	2:61–98	2:52–62	2:73–80		24:70–148	2:72–91
Mormyrops mariae (Schilthuis) 1891	6:112–265	2:135–150		5:87–175	4:142–274			8:30–289	3:194–288
Mormyrops engystoma Boul. 1898	7:76–156	33:57–160	3:91–159	47:35–168	34:59–160	1:97		2:120–125	5:68–137
Mormyrops masuianus Boul. 1898	3:85–196								
Mormyrus proboscirostris Boul. 1898	1:154							1:189	
Mormyrus bumbanus Boul. 1909	7:27–107	1:44	2:64–115					3:81–102	11:90–179
Mormyrus cyaneus new species				2:70–102				3:90–133	47:45–260
Mormyrus iriodes new species				1:86	4:217–270			1:73	15:62–160
Myomyrus macrodon Boul. 1898	1:61	2:52–55	21:18–135	49:22–148	14:42–136			43:20–183	25:40–209
Myomyrus pharao Poll & Taverne 1967	1:71	3:59–82	2:18–60	23:18–129	4:45–66			12:32–68	4:55–83
Petrocephalus simus (Sauvage) 1878	19:40–72	2:44–74		3:54–58	6:48–54				
Petrocephalus grandoculis Boul. 1920		1:58							
Pollimyrus plagiostoma (Boul.) 1898	2:107–108			3:159–172					12:69–150
Stomatorhinus sp. or spp.	3:65–90	21:17–72	36:25–94	179:27–92	80:18–86	5:16–45		34:23–96	40:19–94
CHARACIDAE									
Alestes macrolepidotus (Cuv. & Val.) 1849	13:17–93	1:63		15:33–66	5:51–64	8:50–76		18:46–151	
Alestes imberi Peters 1852		6:30–51	2:34–47			1:30	1:61	2:39–61	6:47–72

Table 3. (Continued)

	R & S 2	R & S 19	R & S 29	R & S 35	R & S 28	R & S 26	R & S 57	R & S 38	R & S 41
Alestes liebrechtsii Boul. 1898			1:99	3:23–41		10:30–54			
Alestes comptus new species									1:55
Bryconaethiops yseuxi Boul. 1899	1:62	5:47–61						2:53–64	6:14–58
Hydrocynus lineatus Bleeker 1862							1:105		
Hydrocynus goliath Boul. 1898			1:39				1:83		
Micralestes acutidens (Peters) 1852						1:53			
Micralestes humilis Boul. 1899	4:22–48		4:41–51			2:30–38		1:46	2:30–47
DISTICHODONTIDAE									
Distichodus mossambicus Peters 1852					1:37			2:53–64	9:81–104
Distichodus antonii Schilthuis 1891	10:57–98	1:64	2:59–65	25:20–101	1:32	8:21–50		3:57–99	7:28–106
Distichodus lusosso Schilthuis 1891			1:52	12:29–48	3:32–42	3:25–29		1:35	2:41–63
Distichodus sexfasciatus Boul. 1897	5:16–43	2:71–78		4:23–47		2:19–23			
Distichodus atroventralis Boul. 1898	1:52			2:22–24		2:24–28			4:33–84
Distichodus fasciolatus Boul. 1898	1:44	1:19	3:42–64	6:24–53	6:33–42			9:35–69	4:39–54
Distichodus maculatus Boul. 1898							1:51		1:81
Nannocharax macropterus Pellegrin 1925	1:31								
CITHARINIDAE									
Citharinus congicus Boul. 1897							1:131		
Citharinus gibbosus Boul. 1899					8:77–128			4:69–120	
Citharinus macrolepis Boul. 1899							1:118		
CYPRINIDAE									
Barbus pleuropholis Boul. 1899					9:33–39				
Barilius weeksii Boul. 1909	1:56								
Barilius lujae Boul. 1909	5:33–98	6:11–14	18:11–34	7:10–16	4:11–24	2:10–20	8:28–33	5:19–89	30:8–77
Chelacthiops elongatus Boul. 1899	1:29		1:36		2:42–48				
Engraulicypris congicus Nich. & Gris. 1917	1:51								
Garra congoensis Poll 1959	8:17–37	3:16–33		7:18–36			1:70		7:38–62
Labeo barbatus Boul. 1898	20:53–103	2:54–77		8:53–80	11:42–70			11:56–74	1:55
Labeo lineatus Boul. 1898	1:173						1:136		2:93–100
Labeo macrostoma Boul. 1898				2:76–81				11:79–125	8:59–217
Labeo velifer Boul. 1898	5:71–173	1:71		2:60–86	3:49–67	2:39–49		5:56–82	1:71
Labeo cyclorhynchus Boul. 1899	1:128								
Labeo nasus Boul. 1899	7:52–158		26:18–57	10:37–91	7:29–78			52:22–158	19:27–201
Labeo variegatus Pellegrin 1901	14:53–89	2:62–68						5:58–82	

TABLE 3. (CONTINUED)

	R & S 2	R & S 19	R & S 29	R & S 35	R & S 28	R & S 26	R & S 57	R & S 38	R & S 41
Labeo greenii Boul. 1902				1:87				1:142	1:121
Labeo weeksii Boul. 1909	1:114								
Labeo sorex Nich. & Gris. 1917	13:27–124	3:26–121	34:19–44					11:35–185	11:58–123
Labeo lividus new species			10:57–89	5:53–89	1:72			4:60–79	6:74–239
Labeo undet. juv.	41:18–38			82:14–30	29:17–25	12:13–24			
Leptocypris modestus Boul. 1902	2:43–50		1:60						
Varicorhinus macrolepidotus Pellegrin 1928									13:100–161
BAGRIDAE									
Auchenoglanis occidentalis (Cuv. & Val.) 1840				2:40–45				1:146	
Bagrus ubangensis Boul. 1902	1:91								
Bagrus caeruleus new species	2:109–210								4:80–164
Chrysichthys cf. *cranchii* (Leach) 1818	3:21–124	4:14–59	3:13–85	29:17–85	5:23–112	5:19–21		37:22–153	4:98–181
Chrysichthys brevibarbus (Boul.) 1899					3:55–91				
Chrysichthys delhezi Boul. 1899	4:81–150	3:46–167		11:51–107	22:27–159		4:71–83	14:64–125	4:131–175
Chrysichthys longibarbus (Boul.) 1899			3:32–34		1:145			1:55	
Chrysichthys helicophagus new species				*6:71–103	2:66–80				1:91
Chrysichthys undet. (very small eyes)					1:81				
Notoglandium pallidum new species			2:20–53	26:19–83	1:73				
Rheoglanis dendrophorus Poll 1966									31:76–320
SCHILBEIDAE									
Eutropius grenfelli Boul. 1900	1:102	1:74							
Schilbe mystus (Linnaeus) 1762							1:85	6:65–103	1:109
AMPHILIIDAE									
Amphilius new species?	1:72			1:69				3:62–86	35:30–90
Doumea alula Nich. & Gris. 1917									47:51–112
Phractura lindica Boul. 1902								3:43–58	124:44–84
CLARIIDAE									
Clarias longibarbus David & Poll 1937	2:68–73	1:102	1:135	1:97			3:70–86		3:59–78
Gymnallabes tihoni Poll 1944			56:46–376	5:93–174				13:61–268	94:33–310
Gymnallabes nops new species				1:57					
Heterobranchus longifilis Cuv. & Val. 1840								1:345	

Table 3. (Continued)

	R & S 2	R & S 19	R & S 29	R & S 35	R & S 28	R & S 26	R & S 57	R & S 38	R & S 41
MALAPTERURIDAE									
Malapterurus electricus (Gmelin) 1789	5:51–69	2:61–62	1:87	1:69	1:91			4:74–105	
MOCHOKIDAE									
Atopochilus guentheri Schilthuis 1891	4:28–89	3:21–135		4:56–106	2:65–67			2:58–70	26:57–230
Atopochilus royauxi (Boul.) 1902	4:69–201								1:185
Chiloglanis congicus Boul. 1920	2:35–40								13:48–87
Chiloglanis carnosus new species			26:21–58	1:32	7:32–47			16:24–58	27:20–61
Synodontis alberti Schilthuis 1891	2:45–50				2:65–74			5:77–93	
Synodontis greshoffi Schilthuis 1891	150:22–86	4:30–80		7:32–53	2:26–32	3:37–45		11:37–90	
Synodontis notatus Vaillant 1893		1:49	1:81				1:49	1:66	
Synodontis pleurops Boul. 1897		1:62							
Synodontis acanthomias Boul. 1899	74:28–125	6:29–104	1:48	9:33–102	11:28–138			2:55–131	
Synodontis caudalis Boul. 1899								1:51	14:52–89
Synodontis decorus Boul. 1899	3:49–86	3:33–60			3:40–46				1:89
Synodontis nummifer Boul. 1899					3:36–59				
Synodontis soloni Boul. 1899	31:26–93	4:27–58	2:48–56	1:55					3:62–74
Synodontis longirostris Boul. 1902			13:53–120	14:41–120	3:50–93			1:79	5:53–79
Synodontis nigriventris David 1936	1:25								
Synodontis brichardi Poll 1959				1:53					13:54–118
CENTROPOMIDAE									
Lates niloticus (Linnaeus) 1762					1:550				
CICHLIDAE									
Haplochromis demeusii (Boul.) 1899			4:35–50	8:35–68	7:16–64	12:12–55		42:22–101	10:16–88
Haplochromis polli Thys 1964	10:19–46								
Hemichromis bimaculatus Gill 1862									1:24
Lamprologus cf. *moquardii* Pellegrin 1903									24:9–50
Lamprologus werneri Poll 1959	24:30–66	17:13–60	3:27–43	72:14–74	80:12–76	5:15–46	6:41–71	220:15–70	14:18–62
Lamprologus lethops new species			2:27–88						
Nanochromis consortus new species									6:26–52
Nanochromis parilus new species		11:11–41	1:31	3:32–42	5:19–42	14:13–44		39:22–44	
Nanochromis minor new species				1:24		3:21–23			
Nanochromis splendens new species				61:13–45	87:14–42	5:9–34		171:16–45	28:15–43
Nanochromis undet.		2:16–29			1:27	2:36–41		4:32–41	1:25

TABLE 3. (CONTINUED)

	R & S 2	R & S 19	R & S 29	R & S 35	R & S 28	R & S 26	R & S 57	R & S 38	R & S 41
Steatocranus gibbiceps Boul. 1899	5:36–46	15:20–42	58:15–80	318:9–75	113:17–54	2:27–29		275:15–68	74:16–84
Steatocranus casuarius Poll 1939	10:12–66	12:20–55		76:10–62	37:15–66	3:20–40		94:15–77	3:14–64
Steatocranus tinanti (Poll) 1939	24:23–44	7:22–36		15:28–44				140:16–55	
Steatocranus glaber new species									19:11–53
Teleogramma gracile Boul. 1899			135:13–65	120:17–71					
Teleogramma depressum new species	18:32–60				17:24–76			64:17–90	19:29–95
Tylochromis lateralis (Boul.) 1898			1:28		14:21–145				
MASTACEMBELIDAE									
Mastacembelus cf. marchei Sauvage 1878				3:286–335	2:316–342				9:134–315
Mastacembelus congicus Boul. 1896	1:153							1:382	3:106–187
Mastacembelus paucispinis Boul. 1899							1:280	1:270	30:60–388
Mastacembelus brachyrhinus Boul. 1899			27:40–142				3:123–126		9:68–164
Mastacembelus brichardi (Poll) 1959	1:114	2:101–106	102:37–139	185:35–122	162:20–133			135:31–140	
Mastacembelus brachyrhinus × brichardi			6:26–145						
Mastacembelus crassus new species			177:35–158	14:54–123	1:75				
Mastacembelus latens new species			3:48–72						
Mastacembelus aviceps new species								17:40–112	10:50–125
TETRAODONTIDAE									
Tetraodon mbu Boul. 1899								1:179	

tion of population samples and re-examination of type material.

Conventions. Unless indicated otherwise in the accompanying text or tables, all measurements of specimen length are of standard length, and all proportional measurements are expressed as percent of standard length. The following abbreviations are used for institutions holding material examined:

MCZ Museum of Comparative Zoology
AMNH American Museum of Natural History
RGMC Musée Royale de l'Afrique Centrale
SU California Academy of Sciences (material formerly at Stanford University)
UMMZ University of Michigan Museum of Zoology.

Campylomormyrus Bleeker 1874

Type species: *Mormyrus tamandua* Günther 1864, by original designation.

Mouth tubular, snout longer than postorbital portion of head. Jaw teeth conical, truncate, or bicuspid, 2–8 in upper and 3–6 in lower jaw. Barbel well-developed. Nostrils closer to eyes than to end of snout. Circumorbital bones five. Lateral ethmoid bone absent. Dorsal fin moderately long, with 26–35 rays, its origin slightly more posterior than anal fin origin. Anal fin as long as, or slightly longer than dorsal fin, with 29–37 rays. Pectoral rays 11 or 12. Lateral line scales 70–95. Vertebrae 45–49.

Bones sharing in the elongation of the snout include the frontals, nasals, parasphenoid, articulars, and dentaries, all extending for almost the full length of the snout. The orbitosphenoid extends into the basal portion of the snout, while the mesethmoid lies distally. The tooth-bearing premaxillary and toothless maxillary bones are very short.

Treated as a synonym of *Gnathonemus* Gill 1862 by Boulenger, *Campylomormyrus* was recognized by Pappenheim (1907a, b) and has been reinstated by Taverne (1968a). Taverne restricted *Gnathonemus* (type species: *Mormyrus petersii* Günther 1862) to species with a moderately elongate snout; terminal or but slightly tubular mouth; fleshy, elongate, cylindrical mentum; four circumorbital bones; and 22–28 dorsal fin rays. Taverne revised the species of *Gnathonemus sensu stricto* and described its osteology. In another paper, Taverne (1968b) described the osteology of *Campylomormyrus* but did not revise the species.

Generic separation of *Campylomormyrus* and *Gnathonemus* is supported by the differences in their habitats. *Gnathonemus* are virtually absent from the largest rivers, occurring rather in secondary tributaries and even small forest streams three to five meters wide. They are also found in backwaters and forest swamps, habitats never occupied by *Campylomormyrus*. In general, the nature of the bottom in *Gnathonemus* habitats is largely determined by the surrounding terrestrial vegetation (usually forest). Submerged tree trunks, branches, and roots, and overhanging banks anchored by roots, are typical features, whereas rocks are absent. We have collected *Gnathonemus* on numerous occasions, but never in association with *Campylomormyrus*.

Campylomormyrus feed predominantly on aquatic insects. Matthes (1964:39) recorded *mirus* from lac Tumba with stomach contents of dead plant debris, decomposing animal debris, and larvae of *Povilla*, chironomids, and odonates. Stomach contents of the 104-mm *mirus* from Wombe, R & S 19, consisted exclusively of trichopteran larvae. A 202-mm *mirus* from Bangui (with a short, stubby barbel) had almost all Chironomidae, with a few trichopterans and small ephemeropterans. The 125-mm *mirus* from Bangui (with an elongate barbel) had trichopterans exclusively. In *rhynchophorus*, a 225-mm specimen from the rivière Mbomou had Simuliidae, Chironomidae, and trichopterans about equally abundant, and a few small ephemeropterans. Of particular interest are the stomach contents of the three large *rhynchophorus* from Luozi. Although their

snout lengths are very different, all three had large numbers of trichopteran larvae and little else in their stomachs; the 376-mm specimen also had a few large ephemeropteran nymphs.

Of the 16 nominal species assigned to *Campylomormyrus* (Taverne, 1972:168–169), 14 are known only from the Zaire basin. Too much emphasis has been placed on snout form and slight differences in scale and fin-ray counts, without allowance for geographical or even individual variation. Population samples have seldom been collected, and most descriptions are based on one or a few specimens only, often either juveniles or exceptionally large adults. Our studies indicate there are only three biologically distinct species: *tamandua, mirus,* and *rhynchophorus.*

Remarks on taxonomic characters

Length. Boulenger, and sometimes Pellegrin and Poll, reported lengths as "longueur totale" without defining this measurement. In some instances (involving fishes other than mormyroids), Boulenger's "longueur totale" is apparently fork length. Lengths of specimens cited by other authors have been quoted to give a general indication of size, and thus no attempt has been made to determine them more precisely. Our own measurements of length are all standard length.

Snout length. Measured from tip of upper jaw to lower margin of eye.

Snout width. Horizontal width of snout taken midway between lower profile of head and tip of upper jaw.

Snout curvature. Measured from tip of upper jaw through middle of eye, expressed as degrees of departure from horizontal axis of body. As horizontal axis of body is often difficult to determine precisely, this measurement is approximate.

Dorsal and anal fin ray counts. These include three unbranched anterior rays, the first of which is small and likely to be overlooked. The last ray, usually thickened and sometimes split to its base, is counted as one.

Longitudinal scale rows. In *Campylomormyrus,* especially *C. rhynchophorus,* it is difficult to make an exact count of longitudinal scale rows. The scales are often covered with thick mucus which is difficult to remove without deranging them. Often the rows are slightly irregular, with gaps or smaller scales interposed, especially along the lateral line. Posteriorly the scales become larger and regularly overlapping, so counting them is relatively easy; but anteriorly scales are small, do not overlap as regularly, and spacing between them is variable. Our counts begin just above or above and slightly behind the gill opening and continue to the end of the hypural fan. They are generally repeatable by us to within five scales. Counts cited by other authors, and quoted here, may in some instances include scales beyond the end of the hypural fan.

Circumpeduncular scale count. This count has been almost invariably cited as 12, 16, 16–18, or 20. In some instances counts of 12 vs. 16 or of 16 vs. 20 were used to distinguish species. We find counts of 12 (occurring in all three species, but less commonly in *rhynchophorus*) are usually straightforward, but that counts above this number are more subjective and highly variable. If one merely doubles the count from top to bottom of the peduncle, counts of 16, 18, and 20 are readily obtained, but this procedure is an oversimplification and

→

Plate 2

a. *Campylomormyrus tamandua*, 128 mm. Ghana, Volta River at Dode (SU 63014).
b–c. *Campylomormyrus tamandua*, 74 mm. Ubangui River at Mobaye (MCZ 48184).
d. *Campylomormyrus mirus*, 113 mm. Bangui market (MCZ 48181).
e. *Campylomormyrus mirus*, 118 mm. Bangui market (MCZ 48181).

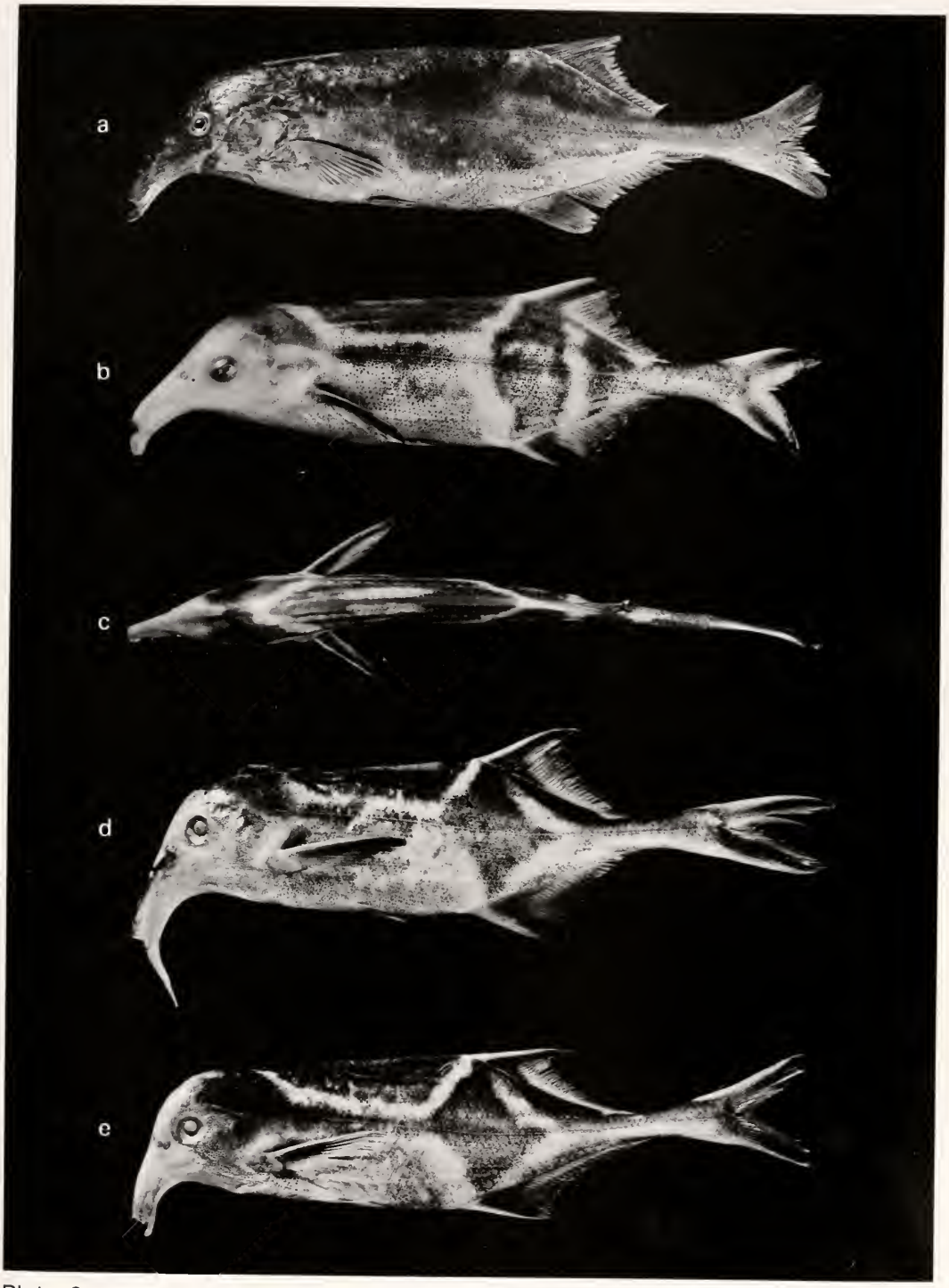

Plate 2

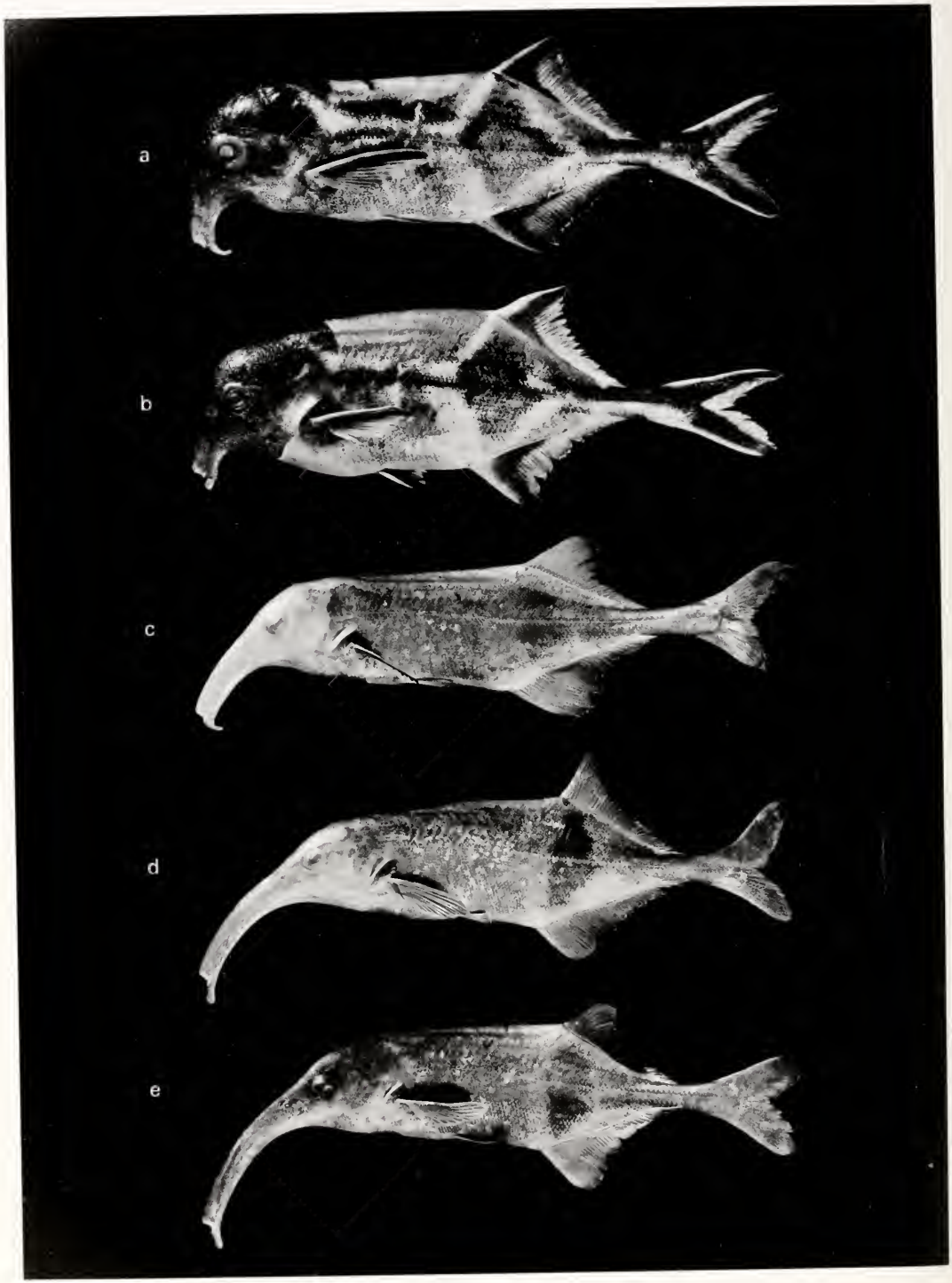

Plate 3

Table 4. Range of variation in some measurements and counts in *Campylomormyrus* over 50 mm in standard length.

	tamandua	*mirus*	*rhynchophorus*
Snout length	13–17	12–20	15–36
Snout width	4.4–6.1	3.8–7.3	2.8–6.3
Snout curvature	36–45°	46–82°	27–60°
Barbel length	2.6–4.4	1.5–18.8	2.1–4.0
Eye diameter	2.5–5.0	2.1–6.4	1.4–5.0
Body depth	21–28	19–34	20–28
LL scales	65–84	68–83	75–95
Peduncular scales	11–13	11–16	12–19
Dorsal fin rays	26–31	31–35	26–34
Anal fin rays	29–35	32–37	29–37

distorts the true variability of the character. In *rhynchophorus*, continuing the count all the way around the peduncle, we find specimens with every number from 12 to 19 (not any with 20, although this number has been reported frequently).

The extent of variation in some characters traditionally used by systematists is indicated in Tables 4 & 5. In *mirus* and *rhynchophorus*, snout length, width, and curvature, eye diameter, and body depth are extremely variable. Variation in form of snout and eye size is greatest among large adults in which the effects of allometric growth are most fully expressed. Depth of body and appearance of snout are markedly affected by "body condition" (apparently related to health and nutritional level). Thus, two specimens of *mirus* with snouts of almost identical length, one apparently in good condition, the other emaciated, were identified by Poll (1967) as different species.

A number of our measurements of snout and eye were taken directly from illustrations in the publications cited.

Campylomormyrus tamandua (Günther) 1864
Plate 2, a–c

Mormyrus tamandua Günther, 1864:22, pl. 2, fig. 1 (West Africa; [= Niger, Boulenger, 1909: 119]).

Diagnosis. Jaw teeth conical or truncate throughout life, never bifid. Snout length 13–17, snout curvature 36–45°; barbel short, 2.6–4.4.

Table 5. Variation in counts of upper and lower jaw teeth in *Campylomormyrus*.

	2+3	2+4	2+5	2+6	3+3	3+4	3+5	4+3	4+4	4+5	4+6	5+3	5+4	5+5	6+3	6+4	6+5	7+3	7+4
tamandua																			
(Ubangui) (n = 6)					3		1	1		1									
mirus																			
mentum long (n = 5)				2		1	1				1								
mentum short (n = 32)	1				3	15	2	1	5			2	1	2					
rhynchophorus																			
S. L. < 100 mm (n = 49)					4	31	2		11				1						
S. L. > 100 mm (n = 38)		1			1	12	1	1	10	2			6		1	1	1		1
Snout length < 25 (n = 21)					1	10	1		4	2			3						
Snout length > 25 (n = 17)		1				2		1	6				3		1	1	1		1

←

Plate 3

a. *Campylomormyrus mirus*, 98 mm. Bangui market (MCZ 48181).
b. *Campylomormyrus mirus*, 90 mm. Rivière Mbomou near Gozobangui, Central African Republic (MCZ 48180).
c–e. *Campylomormryus rhynchophorus*, 140, 172 and 168 mm. Rivière Mbomou near Gozobangui (MCZ 48182).

Coloration. This species exhibits a remarkable geographical color variation which has not been previously recorded. In the Volta basin, *tamandua* are usually uniformly dark brownish or even blackish, sometimes with a subtle violaceous quality (as in all mormyrids, mucus may alter coloration, generally by dulling it and at times providing a yellowish or greenish yellow caste), and no dark or light marks at all (Plate 2, a). In some specimens from the Volta, however, a dark or dusky lozenge-shaped mark extends from the origin of the dorsal fin to the middle of the anal fin base (such a mark occurs in many species of Mormyridae); specimens from the Benue River have similar coloration (Howes, personal communication). In the Zaire basin, *tamandua* are much more strikingly colored (Plate 2, b–c). The lozenge-shaped dark area on the posterior half of the body is always present, and its contrast enhanced by well-defined white bands framing it; anterior half of body with two white bands extending forward in parallel from the lozenge, diverging at the level of the pectoral fin insertion, the upper band passing obliquely forward along the nape, the lower obliquely downward across the margin of the gill opening. Dorsal surface of head and body with separate, paired, longitudinally oriented white marks (Plate 2, c); such marks are unrecorded for any other species of Mormyridae. In addition to our material from the Ubangui reported upon here, the American Museum of Natural History has numerous specimens from the Zaire basin, all with the distinctive coloration.

Range, habitat. This is the most widely distributed *Campylomormyrus*, present in the Volta, Niger, and Chad basins as well as the Zaire basin. In the Zaire basin, it has not been recorded from above Stanley Falls. Our specimens were all collected in or near rapids of large rivers. Although we did not collect this species in the mainstream of the Lower Zaire River, it is to be expected there. In the Upper Niger, where

TABLE 6. VARIATION IN *CAMPYLOMORMYRUS TAMANDUA*.

Locality	SL. mm	Snout length	Snout curv.	Eye diam.	Jaw teeth	LL scales	Ped. scales	Dorsal rays	Anal rays	Reference or cat. no. (no. of specimens)
Niger	ca. 250	17	43°	4.8	4 + 4	80	12	28	31	Günther, 1864 (holotype)
Upper Niger	72–178	15	44°	3.2	2–3 + 4	78–80	12	28–31	33–35	Daget, 1954
Chad basin	?–430	13–16	37–45°	2.5–3.4	2–4 + 3–4	80–84	12	29–30	32–34	Blache, 1964
Volta	114–173	15–17	43–50°	3.2–3.8	3 + 3–4	76–79	12	28–29	31–33	SU 63014 (7)
Ubangui	74–133	14–16		3.4–5.0	3–4 + 3–5	65–75	11–13	26–29	29–32	MCZ 48184-7 (6)

it is rare, it seems to occur only in portions of the mainstream with rocky bed (Daget, 1954:83). The report of Pappenheim (1907a) of *tamandua* from the Sanaga River is apparently based on an emaciated *rhynchophorus* with the snout much longer than in any *tamandua*.

Campylomormyrus mirus (Boulenger) 1898
Plates 2, d–e and 3, a–b

Gnathonemus mirus Boulenger, 1898:11–12, pl. 3, fig. 2 (Upoto, mainstream of Middle Zaire River below mouth of Itimbiri).
Gnathonemus elephas Boulenger, 1898:12, pl. 4, fig. 1 (Upoto).
Gnathonemus christyi Boulenger, 1920:13–14, fig. 4 (Leopoldville [= Kinshasa]).
Gnathonemus alces Boulenger, 1920:14–15, fig. 5 (below Stanley Falls).
Gnathonemus cassaicus Poll, 1967:77–78, fig. 26 (rio Luachimo at Dundo, Angola).

Diagnosis. Barbel length extremely variable, 1.5–18.8; this is the only species capable of developing an extremely elongate barbel (Plate 2, d). Jaw teeth bicuspid or truncate in juveniles and half-grown individuals, truncate or feebly notched in large adults. (In smaller specimens wear may obscure the tooth morphology, which can be verified by dissecting out one or more of the replacement teeth.) Snout length 12–20, curvature 46–82°. This is the only species in which the snout may point nearly straight down.

Snout. Length, width, and curvature of snout highly variable. The extremes in snout length are represented by the holotypes of *alces* (13) and of *christyi* (20). The recorded range of variation of snout length in *mirus* (Table 7) is now virtually continuous between these extremes. The widest snouts are in specimens with markedly elongate barbels, because of the well-developed musculature mobilizing the barbel. This musculature is feebly developed in specimens with short barbels. The 390-mm specimen from the Ja River figured by Steindachner (1914) has an exceptionally long barbel and a wider snout

TABLE 7. PROPORTIONAL MEASUREMENTS, SNOUT CURVATURE, AND COUNTS IN *CAMPYLOMORMYRUS MIRUS*.

Locality	No. of spec.	Length (mm)	Body cond.	Snout length	Snout width	Snout curv.	Length mentum	Eye diam.	Dorsal rays	Anal rays	LL scales	Ped. scales	Reference or cat. no.	Nomenclatural status or other comments
Upoto	1	320	ave.	19	5.6	55°	14.5	3.5	34	35	78	12?	Boulenger, 1898	Holotype of *mirus*.
Upoto	?	400	ave.	17	4.9	60°	1.7	3.3	31–35	33–37	70–80	12?	Boulenger, 1898	Types of *elephas*.
Kinshasa	?	320–375	ave.	20	4.4	82°	2.4	3.6	32–33	34–35	75–80	12	Boulenger, 1920	Types of *christyi*.
Stanley Falls	?	255–330	ave.	13	4.6	71°	3.7	4.8	31–34	33–35	70–75	12	Boulenger, 1920	Types of *alces*.
Dundo, rio Luachimo	2	113–169	ave.	20	6.5	50°	5.1	3.7	31	35	76	16	Poll, 1967	Types of *cassaicus*.
Riv. Ja, Cameroun	1	390	ave.	19	7.3	46°	18.8	2.6	31	34	83	12	Steindachner, 1914	Identified as *mirus*.
Rio Muita, Angola	1	250	thin	14	4.6	60°	3.4	3.4	31	34	75	12	Poll, 1967	Identified as *elephas*.
Rio Luachimo, rio Luendo	?	129–183	ave.	13.5	4.8	57°	2.1	4.2	32–34	34–35	80–81	12	Poll, 1967	Identified as *alces*.
Bangui market	3	112–136	ave.	19–20	5.8–6.2	61–63°	11.0–12.8	5.0	34	33–35	76–80	11–12	MCZ 48181	Resemble type of *mirus*.
Bangui market	14	98–202	ave.	15.5–18	3.8–5.9	55–75°	1.5–5.5	3.8–6.4	31–35	32–36	73–81	11–12	MCZ 48181	Resemble *elephas* & *christyi*.
Riv. Mbomou, Ubangui	4	57–90.5	plump	16–17	5.6–7.9	57–63°	2.6–3.1	5.2–5.5	31–32	32–34	68–72	12	MCZ 48180	Suggestive of *alces*.
Wombe, Lower Zaire R.	1	104	ave.	18	5.3	67°	5.0	5.2	33	35	72	12	MCZ 50165	
Luozi, Lower Zaire R.	1	265	ave.	15.5	4.6	55°	5.3	2.1	32	35	80	12	MCZ 50566	

than any other specimen. The extremes in snout curvature are represented by this specimen from the Ja (46°) and the holotype of *christyi* (82°). Specimens with elongate barbels have the least curvature.

Barbel. A series of *mirus* obtained at the Bangui market in June, 1971 includes three specimens in which the barbel is markedly elongate. In these as well as in the holotype of *mirus* and Steindachner's specimen from the Ja, the barbel is finely tapered. In the other 14 specimens from the Bangui market the barbel is either short and stubby or only slightly elongate. In several it shows signs of mutilation. In one of the Bangui specimens and in a 265-mm specimen from Luozi, the barbel is moderately elongate, with a tapered tip arising from a thickened basal portion, suggestive of partial regeneration toward a markedly elongate condition. On the other hand, it would appear normal for some individuals (including those with a very short snout) not to develop a markedly elongate barbel.

Color pattern. Color pattern as in Zaire *tamandua,* except dorsum between tip of snout and dorsal fin origin uniformly dark (without pairs of elongate light marks on head and midway between tip of snout and dorsal fin origin). Contrast between light and dark areas on both body and fins tends to be sharper than in *tamandua.* Contrast declining with growth, but basic features of color pattern plainly visible in a 265-mm specimen from Luozi.

Range, habitat. C. mirus is widely distributed in the Zaire basin. A specimen from the Benue River reported by Pappenheim (1907a) as *Campylomormyrus* ? *elephas* is almost certainly a *tamandua.* All reports pertaining to *mirus* are of specimens from the Zaire basin. Nichols and Griscom (1917:672) reported specimens from Avakubi, Faradje, Poko, and Stanleyville, all localities near large rivers with rocky beds, and noted that "quite a number were taken with poison in the stony sections of the Dungu River at Faradje." Matthes (1964:39) described the habitat of *elephas* as "lacs, grosses rivières, de préférence sur les fonds rocheux (latérite, au lac Tumba)"; his record of two large specimens from lac Tumba near Mabali is the only well-documented report of *Campylomormyrus* from a lake. The American Museum of Natural History has a 285-mm specimen, probably purchased from fishermen or market women, from "Lake Tanganyika," obtained 9 March by H. C. Raven (AMNH 11710).

Remarks on synonymy

elephas. The type specimens of *elephas,* except for their stubby barbels, are similar to the holotype of *mirus.* Boulenger (1898: 11) distinguished the two species as follows:

D. 34; A. 35; longueur du museau 3 fois son moindre diamètre vertical; appendice du menton mesurant les 3/4 de la longueur du museau. . . . . *mirus*

D. 33; A. 34–36; museau dirigé en bas, sa longueur 3 à 4 fois son moindre diamètre vertical; appendice du menton environ aussi long que l'oeil. . . . . *elephas*

Apart from the difference in barbel, which is variable in *mirus,* the key characters are virtually identical. This is a good example of the narrow typological approach to species formerly in vogue in this group, and no one in the ensuing years since Boulenger proposed a better way to distinguish these two species.

cassaicus. The 169-mm holotype of *cassaicus* closely resembles our specimens of *mirus* with elongate barbels from Bangui, except that its barbel is only moderately elongate. In particular, the length, width, and curvature of the snout, as well as the proportions of the caudal peduncle, are closely similar, and the color pattern is typical of *mirus.* The circumpenduncular scale count of 16 is unusual for *mirus.* Specimens examined by us have 11 or 12.

Campylomormyrus rhynchophorus (Boulenger) 1898
Plates 3, c–e and 4, a–d

Gnathonemus rhynchophorus Boulenger, 1898:12–13, pl. 5, fig. 2 (Upoto).
Gnathonemus curvirostris Boulenger, 1898:13–14, pl. 6, fig. 1 (Matadi).
Gnathonemus numenius Boulenger, 1898:14, pl. 6, fig. 2 (Upoto).
Gnathonemus ibis Boulenger, 1902:25, pl. 4, fig. 5 (Banzyville, Ubangi).
Gnathonemus phantasticus Pellegrin, 1927:299–300 (Nanga Eboko, Sanaga R.).
Gnathonemus compressirostris Pellegrin, 1928a: 17–18, fig. 8 (Boma).
Gnathonemus rhynchophorus luapulaensis David and Poll, 1937:205, fig. 7 (rivière Luapula at Kabunda) (elevated to species by Poll, 1967).
Gnathonemus rhynchophorus lualabaensis David and Poll, 1937:206, fig 8 (Kabelwe [rivière Lufira?]) (elevated to species by Poll, 1967).
Gnathonemus bredoi Poll, 1945:49–50, fig. 5 (Pweto, "lac Moero").
Gnathonemus tshokwe Poll, 1967:83–84, fig. 29 (rio Luachimo at Dundo, Angola).

Diagnosis. Snout extremely variable in length and curvature, usually far longer than in any *tamandua* or *mirus;* barbel short, 2.1–4.0. Teeth invariably conical, even in large adults, unless truncated by wear. Scales relatively small: lateral line scale count about 75–95, circumpenduncular 12–19 but usually 16–19 (versus 84 or less and 11–13 or 16 in *tamandua* and *mirus*). Coloration plain compared to *mirus* and Zaire *tamandua.*

Counts and measurements of *rhynchophorus* are presented in Tables 8 and 9. Because so many nominal species have been placed in synonymy by us, the data are rather extensive. The two large series of specimens from Ubangui played a major role in the development of our concept of *rhynchophorus.* Both series exhibit extreme variability in eye size and snout length; some specimens resemble the types of *curvirostris, ibis, compressirostris,* or *tshokwe,* but there is gradation among these specimens and still others which resemble the types of *rhynchophorus.* Also of importance was the material from the Lower Zaire River, and especially the three large specimens from Luozi and one large specimen from Tadi (Plate 4). The snouts of these four differ so strikingly that a narrowly typological approach would dictate placing each in a separate species, but we are convinced they belong to just one species, *rhynchophorus.*

Dentition. In *rhynchophorus,* as in *tamandua,* the upper and lower jaw teeth are invariably conical, never bicuspid, and only truncate as a result of wear. Data on tooth counts are presented in Table 5. Specimens under 100 mm in standard length exhibit the least variation in tooth counts, with a strongly modal count of 3 + 4 (in 31 of 49 specimens). Specimens over 100 mm have a much greater range of tooth counts, and proportionately fewer specimens with 3 + 4 (12 of 38). The greatest variation in tooth counts occurs in specimens over 100 mm with snout lengths in excess of 25 percent of standard length (only two of 17 with 3 + 4). Examination of the data shows that virtually all of the increased variability in tooth counts in specimens over 100 mm is attributable to the moiety of specimens with the longest snouts. In specimens with snouts over 25, the upper jaw teeth number from 2 to 7, with few specimens having 3, whereas in specimens with snouts under 25 the variation in tooth counts is closely similar to that in specimens under 100 mm, with a strongly modal count of 3 + 4.

Color pattern. Posterior half of body marked by a dark, vertical band, elliptical in shape, and flanked anteriorly and posteriorly by narrow light bands. Anterior light band extends between origin of dorsal fin and origin of anal fin but does not continue onto fins. Caudal peduncle, fins, and anterior half of body more or less uniformly dark. Obvious in juveniles, the contrast between light and dark areas diminishes with growth, until in the largest specimens the banding has disappeared.

Range, habitat. C. rhynchophorus occurs in the Sanaga River and in large rivers in the upper, middle, and lower portions of

TABLE 8. PROPORTIONAL MEASUREMENTS, SNOUT CURVATURE, AND COUNTS IN *CAMPYLOMORMYRUS RHYNCHOPHORUS*.

Locality	No. of spec.	Length (mm)	Snout length	Snout width	Snout curv.	Eye diam.	Jaw teeth	Dorsal rays	Anal rays	LL scales	Ped. scales	Ref. or cat. no.	Nomenclatural status or other comments
Upoto, Middle Zaire R.	4	?–380	22	4.8	54°	2.9	5+4	28–31	31–35	75–85	18	Boul. 1898	Types of *rhynchophorus*.
Matadi, Lower Zaire R.	1	370	28	3.5	60°	1.9	3+4	32	36	90	16	Boul. 1898	Holotype of *curvirostris*.
Upoto	2	?–610	36	2.7	"25°"	2.3	7+4–6	32	36	79–81	16	Boul. 1898	Types of *numenius*.
Banzyville, Ubangui R.	2	150	26	2.3	56°	5.0	6–8+4	32–33	36–37	77–82	16	Boul. 1902	Types of *ibis*.
Nanga Eboko, Sanaga R.	1	440	>25?				3+5	28	31	80	12	Pell. 1927	Holotype of *phantasticus*.
Boma, Lower Zaire R.	1	165	15	3.5	55°	2.9	3+4	30	36	90	16	Pell. 1928a	Holotype of *compressirostris*.
Kabunda	1	170	>25?					29	33	82	16	David & Poll, 1937	Holotype of *r. luapulaensis*.
Kabelwe	1	97	<25					30	33	82	20	David & Poll, 1937	Holotype of *r. lualabaensis*.
Pweto	1	370	18	6.3	27°	3.2	3+5	27	30	"ca. 105"	20	Poll, 1945	Holotype of *bredoi*.
Dundo, rio Luachimo	1	268	30	4.4	48°	2.7	3+3	31	35	86	20	Poll, 1967	Holotype of *tshokwe*.
Rio Luachimo	4	107–170	26	5.2	48°	3.7	4–5+4–6	31–34	33–36	83–90	16–18	Poll, 1967	Identified as *rhynchophorus*.
Rio Luachimo	1	298	33	3.6	40°	2.8	6+4	31	35	85	16	Poll, 1967	Identified as *ibis*.
Rio Muita, Angola	1	220	24.5	5.8	69°	3.9	5+4	30	33	±81	16	Poll, 1967	Identified as *luapulaensis*.
Sakbayeme, Sanaga R.	3	219–249	18–20	4.0–5.3	40–67°	2.6–3.0	3–4+4	29–30	33–35	76–84	12–14	MCZ 35427, 47022	Resemble type of *rhynchophorus*.
Riv. Mbomou, Ubangui	24	43–225	19–32	4.4–7.6	33–56°	2.6–5.9	3–5+3–5	29–31	31–35	77–90	14–19	MCZ 48182	Gradation among specimens resembling types of *rhynchophorus*, *ibis*, *compressirostris*, *tshokwe*.
Bangui market	11	110–282	20–33	3.3–4.9	47–56°	2.5–4.5	3–7+3–5	30–33	32–37	78–95	12–19	MCZ 48183	Gradation among specimens resembling types of *rhynchophorus*, *curvirostris*, and *ibis*.
Gombe, Lower Zaire R.	6	48–113	15–21	4.7–6.1	45–53°	3.2–4.8	3–4+4–5	27–29	29–35	75–85	13–16	MCZ 50104	
Wombe, Lower Zaire R.	8+1	63–135 (130)	16–20 (31)	4.5–5.2 (3.6)	50–52° (53°)	3.5–4.3 (4.7)	3–4+3–5 (6+4)	27–32 (34)	29–33 (37)	82–84 (80)	15–16 (12)	MCZ 50166	130-mm specimen resembles type of *ibis*.
Bulu, Lower Zaire R.	2+1	105–169 (122)	17–19 (30)	4.4–5.3 (3.9)	47–48° (55°)	3.0–3.8 (4.3)	3+4 (4+4)	29 (32)	33 (37)	79–85	16–17 (13)	MCZ 50213	122-mm spec. resembles *ibis*; 105- & 169-mm specs. resemble *compressirostris*.
Luozi, Lower Zaire R.	1	321	16	3.7	40°	2.0	3+4	30	33	±95	13	MCZ 50567	Resembles *tamandua* except for higher LL scale count if large *tamandua* lack color pattern typical of juveniles and young adults.
Luozi	1	376	25	3.2	55°	1.4	3+4	32	36	±90	14	MCZ 50567	Resembles holotype of *curvirostris*.
Luozi	1	445	26	4.2	60°	1.6	2+4	30	37	±95	12	MCZ 50567	Resembles holotypes of *phantasticus*, *tshokwe*.
Tadi, Lower Zaire R.	1	365	32	3.5	55°	1.8	3+4	31	34	90	12	MCZ 50262	
Isangila, Lower Zaire R.	1	105	22	5.0	48°	4.2	5+4	32	36	81	16	MCZ 50404	Resembles holotype of *rhynchophorus*.
Inga, Lower Zaire R.	26	41–99	14–19	4.8–7.4	30–54°	3.6–5.7	3–5+3–4	26–31	31–35	76–85	15–18	MCZ 50423 & 50492	

Table 9. *Campylomormyrus rhynchophorus*. Variation in anal fin ray counts compared to snout length (specimens over 100 mm).

Snout length < 25 (n = 21)	1	1		6	7	4	2		33.76
Snout length > 25 (n = 17)		1	1	5	2	2	2	4	34.47
Number of anal fin rays	30	31	32	33	34	35	36	37	Ave.

the Zaire basin. Specimens collected by us have all come from rapids or sections of rivers with rocky or stony beds. Nichols and Griscom (1917:672–673) reported specimens from Avakubi, Faradje, Poko, Rungu, and Stanleyville, localities all on or near large rivers with rapids or coarse substrates, and specimens reported by Poll (1967) from Angola are almost all from rapids in the rio Luachimo. The Sanaga is a river noted for rapids; Sakbayeme is situated just below a long series of rapids, and Nanga Eboko just above another long series of rapids which includes the Chutes d'Etok. The type locality of *luapulaensis* is near Mambirima Falls, and the type locality of *lualabaensis* is presumably on or near the rivière Lufira, a Lualaba tributary noted for rapids. Pweto, the type locality of *bredoi*, is at the north end of lac Moero at the point where the lake is drained by the rivière Luvua. Major rapids occur within 20 or 30 km of Pweto, and large river habitat with coarse substrate probably occurs very close to town. If the type specimen was purchased at Pweto, it may well have come from the river. The species has not been reported from any other lacustrine locality.

C. rhynchophorus is not uniformly distributed in the mainstream of the Middle Zaire River. It is absent from the list of mormyrids from large river habitats in the vicinity of Ikela reported by Matthes (1964: 9). We do not have any information as to whether the streambed is rocky or stony at Upoto. It is generally supposed that rocks and stones are absent from streambeds in the Cuvette Centrale, but this need not necessarily be so. It is noteworthy that piles of large lateritic rocks occur along substantial portions of the shores of lac Inongo and lac Tumba.

Comment. A population sample from rapids in the rivière Mbomou, a tributary of the Ubangui River, yielded three *tamandua*, four *mirus*, and 24 *rhynchophorus*. The *rhynchophorus* have extremely variable snouts, but there is no indication whatever of intergradation among the three species. Data on these specimens are included in Tables 6–8.

Remarks on synonymy

numenius, ibis. The 610-mm holotype of *numenius* is the largest recorded specimen of *Campylomormyrus*. The unusually "straight" condition of its snout requires comment. No juveniles have been reported with the snout directed almost straight ahead. During six months of almost daily visits to the market in Kinshasa in 1963–64, the senior author observed numerous large specimens with the characteristic appearance of *numenius*, and determined that straightening of the snout was in all instances due to the manner in which the fish had been handled. Straightening occurs when fish are caught by a hook through the end of the snout; hefted or carried about by the snout; or laid out for sale by market women. Had this been known to Boulenger, he could hardly have failed to recognize the 150-mm holotype of *ibis* as a young *numenius*. The descriptions and figures of *numenius* and *ibis* agree closely except for the condition of the snout; in *ibis* the snout has been bent slightly backward. The difference in eye size is attributable to allometric growth. In *rhynchophorus*, as in many other mormyrids, the eye is relatively larger in young.

Plate 4

Nichols and Griscom (1917:672–673) reported *rhynchophorus* and *ibis* from Avakubi, Faradje, Poko, and Stanleyville (= Kisangani). They found the proportions of the snout variable in *ibis* (generally longer and more slender in large specimens), and concluded "it is difficult to draw the line between *rhynchophorus* and *ibis*, which are at best closely related." This conclusion is supported by our observations, which indicate they are indeed conspecific.

curvirostris, ibis, tshokwe. Except for its larger eye, the 268-mm holotype of *tshokwe* is very similar to the 370-mm holotype of *curvirostris*, as well as to the 298-mm specimen identified by Poll (1967) as *ibis*. Poll (1967:85) tabulated the following differences among the three species:

	curvirostris	*ibis*	*tshokwe*
Longueur museau/ hauteur minimum	11	8–12	8.5
Longueur museau/oeil	15	9	9
Longueur peduncule caudal/hauteur minimum	3.7	3	2.7
Ecailles peduncule caudal	16	16	20
Ecailles en l. l.	86	77–82	86

The information in this table is based on extremely few specimens—only one each of *curvirostris* and *tshokwe*—so that it does not allow for any variation. The characters, involving snout form, eye size, length and height of caudal peduncle, and scale counts, are subject to considerable individual variation in *Campylomormyrus*. In several samples of *rhynchophorus*, for example, circumpenduncular scale counts range from 14–19 or even 12–19, and longitudinal scale counts from 76–95. Poll (1967:67) stated that *ibis* might be a junior synonym of *curvirostris*, a conclusion supported by our observations. The two species have been distinguished chiefly on the basis of *curvirostris* having a smaller eye. Eye diameter varies from 1.4 to 5.0 in *rhynchophorus*, with large adults much more variable than juveniles due to allometric growth. Poll's data on the holotype of *tshokwe* agrees fairly closely with that which he presented for *ibis*, and thus it seems he had insufficient grounds to recognize *tshokwe* as new.

compressirostris. The holotype of *compressirostris* is representative of *rhynchophorus* with the snout at its shortest and most slender. Apart from snout length, no other characters have been advanced which will separate it from other nominal species synonymous with *rhynchophorus*. Some small series from the Lower Zaire mainstream are comprised mainly of such short-snouted individuals. They exhibit considerable variation in eye size. Their dorsal and anal fin-ray counts fall within the lower half of the range of these counts in *rhynchophorus*. David and Poll (1937: 206) considered *compressirostris* a subspecies of *rhynchophorus*.

phantasticus. The length, thickness, and curvature of the snout in the 440-mm holotype of *phantasticus* is virtually identical with that in a 445-mm specimen of *rhynchophorus* from the Lower Zaire River at Luozi. A photograph of the anterior half of the holotype (Pellegrin, 1932) also shows 20–21 scales to the end of the pectoral fin and 8–9 scale rows above the lateral line immediately behind the head, counts which occur in *rhynchophorus* from the Zaire basin. Other characteristics of the holotype are well within the range of variation for *rhynchophorus*. Additional material from the Sanaga River collected by George Schwab (MCZ 35427, 47022) is closely similar to material from the Zaire basin.

bredoi, luapulaensis, and lualabaensis. C. bredoi is known only from the 370-mm

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Plate 4

a–c. *Campylomormyrus rhynchophorus*, 321, 445 and 376 mm. Zaire River at Luozi (MCZ 50567).
d. *Campylomormyrus rhynchophorus*, 365 mm. Zaire River at Tadi, about 50 km downstream from Luozi (MCZ 50262).

holotype obtained at Pweto. The holotypes of *luapulaensis* and of *lualabaensis* are the only other specimens of *Campylomormyrus* recorded from the Zaire basin above Stanley Falls. The exceptionally short and stocky snout of *bredoi* is unlike that in any other specimen reported in the literature or seen by us. Although Poll (1945) reported around 105 scales in the longitudinal series, the figure shows only about 90 scales to about where the end of the hypural should be and only 98 scales continuing well beyond this point onto the caudal fin. It should be noted that the 97-mm holotype of *lualabaensis* was characterized by an unusually short snout. Many specimens of *rhynchophorus* have the snout as short as in *lualabaensis* and *bredoi*, but only some with elongate snouts have the snout as wide as that of *bredoi*. In *luapulaensis* the snout is elongate and wide. These observations indicate that populations of *rhynchophorus* in this part of the Zaire basin are also subject to considerable individual variation in snout length and form.

Mormyrus Linnaeus 1758

Type species: *Mormyrus caschive* Linnaeus 1758 (ex Hasselquist 1757).

Mormyrus is distinguished from all other mormyrid genera by its long dorsal fin (originating on or in front of a vertical line through insertion of pelvic fins), in combination with an extremely short anal fin. The osteology of *Mormyrus* is compared with that of other genera by Taverne (1972). Some 20 species have been described (op. cit.: 163–164). Those in the Zaire basin have been revised by Reizer (1964). There are four species in our rapids collections, two of them new.

Mormyrus cyaneus new species
Plate 5, c

Holotype. MCZ 50497, 153.2 mm, R & S 41.
Paratypes. MCZ 50498, 46: 45.4–260 mm, R & S 41; MCZ 50430, 3: 90.3–132.6 mm, R & S 38; MCZ 50266, 2: 69.8–101.7 mm, R & S 35.

Diagnosis. A *Mormyrus* with a distinctively shaped snout, more elongate than the snout of *bumbanus* (Plate 5, d) but not nearly as elongate and slender as the snout of *rume* or *proboscirostris*. Coloration uniformly light blue, or uniformly blue on the body with the head dark blue or blackish blue; no iridescence. Dorsal rays 51–59, with a lower mode and mean than other *Mormyrus* from the Lower Zaire River (Table 10), or from anywhere else.

Mormyrus iriodes new species
Plate 5, e

Holotype. MCZ 50499, 160.1 mm, R & S 41.
Paratypes. MCZ 50500, 14: 62.2–151.5 mm, R & S 41; MCZ 50354, 4: 217–270 mm, R & S 28; MCZ 50431, 1: 72.7 mm, R & S 38; MCZ 50267, 1: 86.5 mm, R & S 35; MCZ 50569, 2: 252–263 mm, R & S 29a.

Diagnosis. A *Mormyrus* similar to the very distinctive species *ovis*, from which it differs in having a much smaller eye and an even more rounded snout, and possibly also in coloration. Live specimens with a pearly iridescence and delicate pinkish, violaceous and bluish-green reflections.

Comment. *M. bumbanus, cyaneus,* and *iriodes* were taken sympatrically at R & S 38, where *proboscirostris* was also present, and at R & S 41. All of the specimens of *Mormyrus* from these localities are readily recognizable as belonging to one or the other of the four species, i.e., there is no intergradation. The differences in the snout are evident in juveniles, which could be

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Plate 5

a. *Mormyrops mariae*, 130 mm, black phase. Zaire River at Inga (MCZ 50462).
b. *Mormyrops mariae*, 117 mm, white phase. Zaire River at Gombe (MCZ 50106).
c. *Mormyrus cyaneus* new species, holotype, 153.2 mm. Zaire River at Inga (MCZ 50497).
d. *Mormyrus bumbanus*, 149 mm. Zaire River at Inga (MCZ 50496).
e. *Mormyrus iriodes* new species, holotype, 160.1 mm. Zaire River at Inga (MCZ 50499).

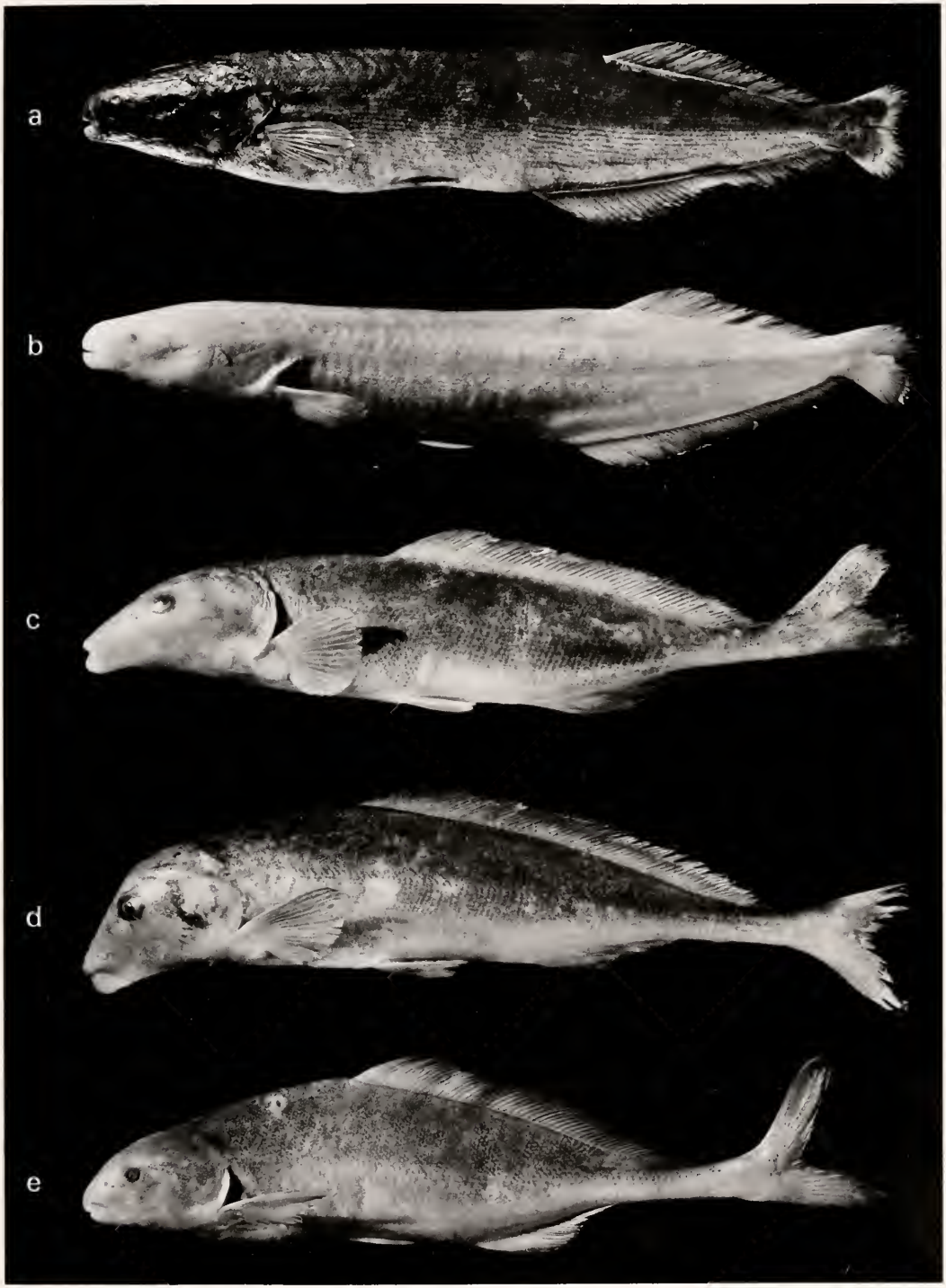

Plate 5

TABLE 10. FREQUENCY OF DORSAL FIN RAY COUNTS IN SEVERAL CLOSELY RELATED SPECIES OF *MORMYRUS* FROM THE ZAIRE BASIN.

	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71
bumbanus (L. Zaire R.)[1]											1	1	1	3	7	4	4		1		
bumbanus (Ubangui)[2]											3		1	1	2	1	1	1	1	1	1
caballus (Cuvette Centrale)[3]							1			1	2		1	4	4	2		2		2	
cyaneus n. sp. (types)	2	3	7	16	9	2	8	3	1												
iriodes n. sp. (types)		1				3	4	4	2	2	2		1								
ovis (Ubangui)[4]				1	3	1				1											

[1] MCZ 50110, 50170, 50217, 50429, 50496. [2] MCZ 48200, 48202. [3] Data from Reizer, 1964. [4] MCZ 48204, 50587.

sorted into their respective species on this basis alone.

Alestes Müller and Troschel

There is a nomenclatural problem regarding the type species of *Alestes*, and the proper generic term for the fishes we refer to under this name should perhaps be *Myletes*, a problem we shall not attempt to solve here. Our rapids collections include four species, one of them undescribed.

Alestes comptus new species
Plate 6, a

Holotype. MCZ 50506, 55.0 mm, R & S 41.
Paratypes. MCZ 48232, 6: 44.8–63.0 mm, market at Bangui, Central African Republic, T. R. Roberts, May–June 1971.

Diagnosis. A moderately deep-bodied *Alestes* with 10 dorsal and 17 anal-fin rays; 23–26 scales in the lateral line series; 15 gill rakers on lower limb of first gill arch; outer premaxillary tooth row with 4 + 4 or 3 + 3 teeth nearly perfectly aligned with each other; coloration distinctive, with no tail-light in live individuals.

A. comptus superficially resembles *A. imberi*, but differs in numerous respects from that species. *A. imberi* taken at the same locality as the holotype, R & S 41, have a slightly wider head; nostrils further apart; a larger mouth; larger teeth; outer premaxillary tooth row with 4 + 4 teeth, but second tooth lying further inside than the others; and 19–20 gill rakers on lower limb of first gill arch. The squamation also differs: *comptus* has 10 predorsal scales (versus 8–9 in *imberi*), and larger and less numerous scales on the base of the anal fin (Figure 2). There are also important differences in coloration. Similar differences exist between the paratypes of *comptus* and specimens of *imberi* obtained at the market in Bangui at the same time.

Coloration. Due to its coloration, *comptus* was recognized as a distinct species the moment it was collected. The entire body is lighter-colored and less dusky than in *imberi*. Live *imberi* are characterized by a tail-light, a highly reflective spot on the dorsal surface of the caudal peduncle, immediately behind the adipose fin. In daylight this spot is usually bright orange. In preserved specimens it is represented by a light-colored, crescent-shaped spot, standing out clearly from the rest of the otherwise dark dorsal surface and from the black spots on the sides of the caudal peduncle which encroach upon it from below. The holotype of *comptus* had no tail-light when it was alive, and the preserved specimen has no indication of one. The dorsal surface, while darker than the rest of the body, is lighter than in *imberi*, and there is no light area atop the caudal peduncle. The black spot on the side of the peduncle is smaller than in *imberi*, and continues as a longitudinal band to the tips of the middle caudal rays. In *imberi* the spot continues onto the caudal base, but extends only half the length of the middle rays. In *comptus* the humeral spot is placed on the fifth,

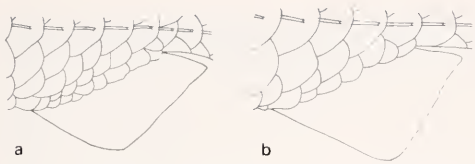

Figure 2. *Alestes*, squamation at base of anal fin: a. *imberi*, 53 mm; b. *comptus*, 55 mm.

sixth and seventh scale rows behind the upper angle of the gill cover, whereas in *imberi* it is on the fourth and fifth scale rows. In the 63.0-mm paratype, after three years in preservative, an iridescent golden band still extends from the eye to the base of the caudal fin; immediately below this golden band, and above the lateral line scales, an iridescent violet and bluish-green band extends from the opercle to a point above the anal fin origin. Such coloration has not been recorded for any other *Alestes*; it is suggestive of the iridescent coloration covering the entire body in mature male *Phenacogrammus interruptus*, a species endemic to the Zaire basin, and one of the most beautiful members of the family Characidae. The condition of the anal fin in this specimen indicates that it may have been taking on secondary male sexual characters.

Bryconaethiops Günther 1873

Type species: *Bryconaethiops microstoma* Günther 1873, by original designation.

Bryconaethiops constitutes a small group of closely related species, one in the Zaire basin and in two or three coastal drainages in Lower Guinea, the others restricted to the Zaire basin. The genus has been distinguished from *Alestes* on the basis of having three rows of premaxillary teeth instead of only two, but this distinction is not well defined. Many *Alestes* have the second tooth in the outer premaxillary tooth row inset, so that it lies between the outer and inner rows and constitutes a third row of the same nature as in *Bryconaethiops*. If the genus is to be retained, it should be defined on the basis of other characters.

Our rapids collections include a single species, previously known only from the holotype and erroneously consigned to synonymy.

Bryconaethiops yseuxi Boulenger 1899 Plate 6, b–c

Bryconaethiops yseuxi Boulenger, 1899: 82–83, pl. 37, fig. 2 (Haut-Congo).

Diagnosis. A small, highly rheophilic species of *Bryconaethiops* with pronounced sexual dichromatism, reduced cuspidation of inner premaxillary teeth, thin lower lip, and 11–13 gill rakers on lower limb of first gill arch.

Differences between *yseuxi* and the other known species of *Bryconaethiops* are summarized in Table 11.

Size at sexual maturity. Males mature at a larger size and grow larger than females. The largest known specimen, the 70-mm holotype, is a male with fully developed secondary sex characters. Our rapids material includes five mature males, 56–64 mm, with fully-developed secondary sex characters, and a 58-mm specimen in which the characteristic male coloration and dimorphism of the dorsal and anal fins are only partially developed. The largest female, a ripe specimen, is 53 mm; a gravid female is only 47 mm.

Coloration of preserved specimens. Females and immature males are very plain: body pale straw color, slightly dusky above (counter-shading); all fins whitish or clear. A faint humeral spot present in both sexes; in highly colored males it is almost obliterated by the general duskiness of the body.

Mature males are striking. Body very dusky. A continuous dark band, almost black, extends on ventral portion of body from behind pectoral fin insertion to end of anal fin base (similar coloration does not occur in any other African characid). Dorsal, pectoral, and pelvic fins dusky, tipped with black (dorsal filaments black). Anal

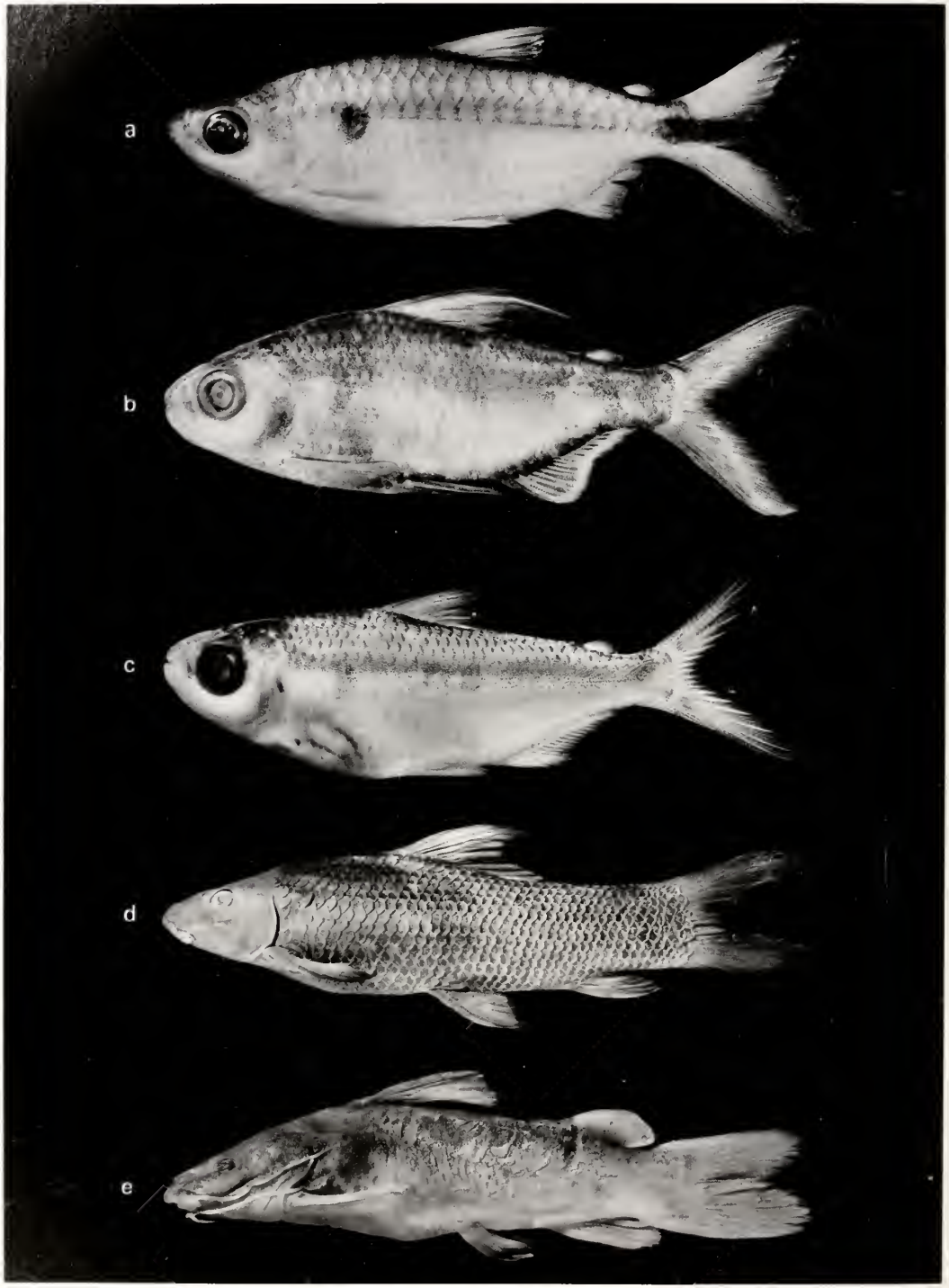

Plate 6

Table 11. Comparison of *B. yseuxi* and other *Bryconaethiops*.

	yseuxi	*microstoma*	*macrops*	*boulengeri*
Longest known standard length.	70 mm	160 mm	110 mm	140 mm
Condition of dorsal fin rays in mature males.	All or almost all prolonged as separate filaments.	As in *yseuxi*.	As in *yseuxi*.	Only anteriormost ray prolonged; none separate.
Sexual dichromatism.	Permanent.	Absent (even seasonally?).	Absent (even seasonally?).	Absent (even seasonally?).
Lower lip.	Thin, leaving premaxillary teeth largely exposed.	Thick, largely covering premaxillary teeth.	Thick, largely covering premaxillary teeth.	Thick, largely covering premaxillary teeth.
Cusps on anterior margin of teeth in inner premaxillary tooth row.	Usually absent.	Always present.	Always present.	Always present.
Number of gill rakers on lower limb of first gill arch.	11–13.	16–19.	17–19.	19–20.

fin with a dusky base, a white submarginal band, and a black margin. Caudal fin uniformly dusky.

Dentition. The small outer premaxillary teeth tend to retain a well-developed lateral cusp which is usually absent in the other species of *Bryconaethiops,* while the enlarged inner premaxillary teeth have lost the anterior cusps that are retained in the other species (Fig. 3).

As in other *Bryconaethiops,* the teeth on the left side of the upper and lower jaws usually lie slightly anterior to those on the right side. The number and size of the teeth, and the number of cusps they bear, are usually the same on both sides of the jaws. In instances in which there is an extra tooth, a larger tooth, or a tooth with more cusps on it, this usually occurs on the left side of the jaws. These statements hold for the upper jaw teeth illustrated in Figure 3. In the holotype of *yseuxi,* the two median teeth in the inner row on the right premaxillary have weakly developed cusps anteriorly, whereas those on the left premaxillary have none (personal communication from Gordon Howes). Such differences may in individual cases be attributable to differential wear on the teeth, but they are usually due to a fundamental bilateral asymmetry favoring the left side of the jaws. In the other species of *Bryconaethiops* the inner premaxillary teeth on both sides of the jaws invariably have well-developed anterior cusps.

Comments. This species was originally distinguished by Boulenger because of the elongate filamentous extensions of the dorsal fin rays in the holotype. Later, evidently recognizing the sexually dimorphic nature of this character, he stated that *yseuxi* was perhaps a synonym of *Bryconaethiops microstoma* (Boulenger, 1916:176). Nichols and Griscom (1917) treated it as a synonym

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Plate 6

a. *Alestes comptus* new species, holotype, 55.0 mm. Zaire River at Inga (MCZ 50506).
b–c. *Bryconaethiops yseuxi*, ♂, 57 mm, and ♀, 47 mm. Zaire River near Wombe (MCZ 50179).
d. *Labeo lividus* new species, holotype, 180 mm. Zaire River at Inga (MCZ 50524).
e. *Chrysichthys helicophagus* new species, holotype, 94.5 mm. Zaire River at Tadi (MCZ 50292).

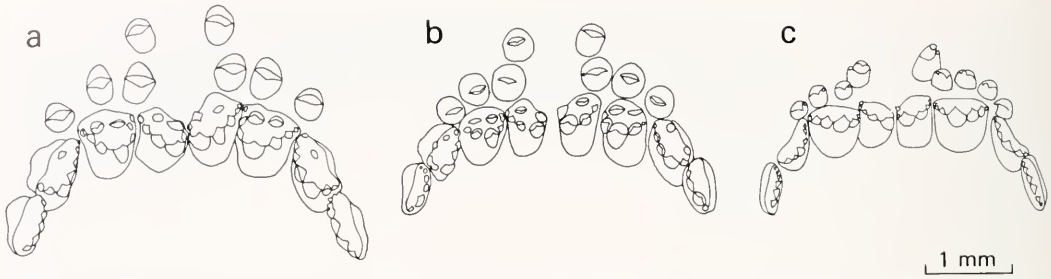

Figure 3. *Bryconaethiops*, premaxillary dentition: a. *microstoma*, 65 mm; b. *boulengeri*, 57 mm; c. *yseuxi*, 57 mm.

of *microstoma*; Poll (1939), evidently without having examined the holotype, concluded that it must be a synonym of either *microstoma* or *macrops*.

Labeo Cuvier 1817

Type species: *Cyprinus niloticus* Forskål 1775.

Our rapids collections include 11 *Labeo*, more species than any other genus except *Synodontis*. One of them is new.

Labeo lividus new species
Plate 6, d

Holotype. MCZ 50524, 180 mm, R & S 41.
Paratypes. MCZ 50525, 5: 74.1–239 mm, R & S 41; MCZ 50452, 4: 60.3–78.9 mm, R & S 38; MCZ 50232, 10: 57.5–87.9 mm, R & S 29; MCZ 50371, 1: 72.4 mm, R & S 28; MCZ 50287, 5: 53.1–89.1 mm, R & S 35.

Diagnosis. A *Labeo* with two pairs of well-developed barbels; barbels dull-colored, of the same hue as the skin of the head where they arise; length of posterior barbel consistently slightly less than diameter of eye, and length of anterior barbel about one-third to one-half that of posterior barbel; keratinous tubercles on head small, granular, white spots which project little or not at all above surface of head; adults dull blue dorsally and laterally, whitish ventrally; 37–39 scales in a lateral series to end of hypural plate, 20–24 (usually 24) around caudal peduncle; dorsal fin with 10 or 11 (usually 11) branched rays, its margin falcate.

Labeo lividus is apparently closely related to *L. barbatus*, which differs from it in having barbels dark or black in color, anterior barbel frequently as long or longer than posterior barbel, both barbels usually longer than eye diameter; eye more nearly superolateral in position; tubercles on head more strongly developed; and adults with back and sides pale-colored or dirty white, with indistinct darker vertical marks on the scales.

Lips. Rostral flap fimbriated. Inner surface of upper lip with numerous transverse plicae formed by minute, confluent papillae. Lower lip with numerous large, conical papillae which become larger and harder with growth. The lips are very similar in *barbatus*, except the papillae on the lower lip apparently do not become quite as large and hard.

Eye. Diameter of eye 4.6–9.4% in specimens from 53 to 239 mm, relative size of eye decreasing with growth. Position of eye lateral or slightly superolateral, less superolateral than in *barbatus*.

Squamation. There are 37–39 scales in a lateral series to end of hypural fan, plus two to four more pored scales extending onto base of caudal fin; 8–11 (usually 11) scales above lateral line; 6–8 (usually 7) scales between lateral line and pelvic fin insertion; and 20–24 (usually 24) scales around caudal peduncle. The dorsomedian scale row anterior to the dorsal fin is poorly developed, the scales small, irregularly positioned, and often with scaleless gaps between them; the first one or two dorso-

lateral scale rows anterior to the dorsal fin are also reduced in size. The squamation of *barbatus* is virtually identical, except that there are usually only 8 or 9 scales above lateral line, and usually 20 or 21 (rarely 24) scales around caudal peduncle.

Juvenile coloration. Except for the striking difference in the barbels, the coloration of juveniles is very similar to that in *barbatus.* The entire sides of the body exhibit a reticulate pattern of light and dark areas, parallel or complementary to the scales. The pattern is very similar in *barbatus*; there may be a difference in that the indistinct darker vertical marks on the scales characteristic of adult *barbatus* are sometimes more evident in juveniles of *barbatus.* The caudal peduncle bears a dark vertical blotch, surrounded by a poorly defined lighter area; two or three scale rows extending onto the caudal fin are also darkened. There is no indication of either red spots on the scales or of a dark midlateral stripe, characteristic features of juvenile coloration in some other species groups of *Labeo.*

Comments. Labeo barbatus and *L. lividus* differ considerably from most previously described *Labeo* with two pairs of barbels (cf. Poll and Gosse, 1963: 52–53). The most closely related species is perhaps *L. capensis,* endemic to the Orange River drainage in South Africa. Juvenile as well as adult *capensis* have distinctive coloration, and adults are further distinguished by a sharply rising nape and strongly compressed head (Jubb, 1967: 123–124, fig. 127, color plate 24). While adults of all three species have a rising nape, the condition is apparently least developed in *lividus,* with *barbatus* intermediate. Other African *Labeo* with two pairs of barbels as adults differ in having fewer scales in a lateral series (mostly 32–34), fewer circumpenduncular scales (usually 16), and different coloration. None of the species with a single pair of barbels as adults (some of which do have two pairs earlier in life) seem closely related to the group under consideration. In the Lower Zaire River the only other *Labeo* in which adults have bluish coloration on the back and sides are *nasus* and *sorex,* species with a median protuberance on the snout tip, and strongly developed tubercles on the head and snout (especially on the protuberance). Most (all ?) other *Labeo* in the Zaire drainage have tubercles more strongly developed than *lividus.*

There is no indication of intergradation between *barbatus* and *lividus* at the four rapids localities where we found them living together.

Bagrus Cuvier and Valenciennes 1839

Type species: *Silurus bayad* Forskål 1775.

Our rapids collections include two species of *Bagrus,* one of them undescribed.

Bagrus caeruleus new species

Holotype. MCZ 50582, 125.7 mm, R & S 41.
Paratypes. MCZ 50527, 3: 80.3–163.5 mm, R & S 41; MCZ 50141, 2: 108.9–210 mm, R & S 2.

Diagnosis. A *Bagrus* with occipital process widely separated from first interneural bone; anal fin with six or seven branched rays; eye small, decreasing in relative size with growth, from 3.7 to 2.6% in specimens from 80 to 210 mm; juveniles as well as adults bluish on the back and sides, with a darkened area in front of dorsal fin (more noticeable in juveniles), undersides of head and abdomen pale, and edges of upper and lower caudal fin lobes whitish.

Bagrus caeruleus is apparently closely related to *B. ubangensis,* which differs from it principally in having a larger eye, and the back and sides brownish, with small black spots (variable in position and number) especially on the adipose and caudal fins. There also seem to be slight differences in the proportions of the head, body depth, and caudal peduncle depth, but in many other respects the two species are quite similar (Table 12).

TABLE 12. DIFFERENCES IN PROPORTIONAL MEASUREMENTS BETWEEN FOUR *BAGRUS UBANGENSIS*, 91–114 MM, AND SIX *B. CAERULEUS*, 80–210 MM.

	caeruleus	*ubangensis*
Length of head (to insertion of gill cover).	28.6–31.1	28.2–29.7
Width of head.	20.4–23.5	19.2–20.2
Interorbital space.	9.2–10.3	8.5– 8.7
Eye diameter.	2.6– 3.7	5.0– 5.7
Width of body (at insertion of pectoral spines).	21.4–23.8	19.8–20.6
Depth of body (at dorsal fin origin).	17.4–20.3	14.1–15.5
Least depth of caudal peduncle.	10.4–11.7	8.2– 8.5

Comments. Apart from *B. docmac* in Lake Tanganyika, the only other nominal species of *Bagrus* in the Zaire basin is *B. lubosicus* Lonnberg 1924, from the rivière Lubozi, a tributary of the rivière Luala, in Lower Zaire. The 243-mm holotype of *lubosicus* should be re-examined to see if it is distinct from *ubangensis*. Its eye diameter, 7½ in head, probably occurs in *ubangensis* of comparable length. The description of its coloration agrees with that of *ubangensis*. Our largest *caeruleus*, 210 mm, has the eye 11 or 12 times in head, depending upon how head-length is measured, and the eye should be even smaller in larger specimens.

Bagrus caeruleus and *ubangensis* were collected together at one of our rapids stations (R & S 2); the differences between the two species are readily apparent in the specimens from this locality.

Chrysichthys Bleeker 1858

Type species: *Pimelodus auratus* Geoffroy Saint-Hilaire 1809, by original designation.

Our rapids collections include six species of the bagrid catfish genus *Chrysichthys*, one of which we shall describe as new. The 81-mm *Chrysichthys* undet. from R & S 35 (MCZ 50378), if its very small eyes are characteristic, is probably also new, but we do not wish to describe it until more material becomes available.

Chrysichthys helicophagus new species
Plate 6, e

Holotype. MCZ 50292, 94.5 mm, R & S 35.
Paratypes. MCZ 50293, 5: 71.4–103.0 mm, R & S 35; MCZ 50377, 2: 66.3–79.8 mm, R & S 28; MCZ 50530, 1: 91.1 mm, R & S 41.

Diagnosis. A small-eyed, snail-eating *Chrysichthys*; dorsal profile of head moderately steep (much steeper than in *delhezi* and *cranchii*, in which the head is relatively depressed, and the mouth broader); palatal teeth restricted to widely separated, small narrow patches; gill rakers on first gill arch 7–8 + 1 + 12–14; color uniformly bluish grey or greyish blue.

Head 31.0–33.5. Eye 4.6–6.4. Snout 12.2–13.6. Interorbital 9.6–10.5. Depth of body 24.3–27.0. Depth of caudal peduncle 12.4–14.2. Dorsal spine 15.8–20.0. Pectoral spine 16.0–19.6. Base of adipose fin 13.4–15.9.

Barbels: nasal, 12.1–16.0; maxillary, 30.5–33.9; inner mandibular, 14.2–19.5; outer mandibular, 22.8–28.4.

Comment. In all six of our specimens of *helicophagus* the guts are well filled with gastropods, which they had ingested whole without crushing the shells: *Potadoma wansoni*, *Bulimus* (*Parabithynia*), and *Cleopatra hargeri*. Other *Chrysichthys* from the rapids usually have no mollusks in their guts; if present at all, they are few.

Notoglanidium Günther 1902

Type species: *Notoglanidium walkeri* Günther 1902, by original designation and monotypy.

Notoglanidium pallidum new species
Plate 7, a–c

Holotype. MCZ 50236, 53.4 mm, R & S 29.
Paratypes. MCZ 50237, 1: 20.2 mm, R & S 29; MCZ 50294, 26: 19.3–82.5 mm, R & S 35; MCZ 50379, 1: 72.7 mm, R & S 28.

Diagnosis. *N. pallidum* is the only *Notoglanidium* which is microphthalmic and

pallid in coloration. It further differs from its congeners in having a greatly depressed head and only 9–10 dorsal fin rays.

Head 29.5–33.6. Eye 1.3–1.6. Interorbital space 5.6–6.5. Maxillary barbel 10.8–16.2, inner mandibular barbel 14.2–28.2, outer mandibular barbel 38.5–47.1. Depth of body 11.8–16.3, width 23.0–24.9. Dorsal spine very short, 3.8–7.2, pectoral spine 9.1–11.5. Base of adipose 18.2–26.8. Predorsal length 35.9–37.7, preanal 66.7–73.1. Caudal peduncle length 16.0–17.8, depth 8.7–10.5. Dorsal fin with 9–10 branched rays, anal 6–8, pectoral 8. Principal caudal rays 7–8 + 9. Branchiostegal rays 8 + 8 (3) or 9 + 9 (1). Postweberian vertebrae 29–31. Coloration in life pallid pink; in preservative light dusky cream-color or greyish.

Comments. This species agrees with *Auchenoglanis* and *Notoglanidium* but differs from *Parauchenoglanis* in having a premaxillary tooth band narrow in lateral extent, large papillae on the lips, and an extremely folded pharyngeal epithelium. In *Parauchenoglanis* the premaxillary tooth band is much wider, the lips are but finely papillose, and the pharyngeal epithelium relatively simple. It differs from *Auchenoglanis* but agrees with *Notoglanidium* in having a dorsal fin with more than seven branched rays, eye without free border, a low adipose fin, and a rounded caudal fin. In many ways it somewhat resembles *Parauchenoglanis boutchangai* Thys 1965, a microphthalmic, dorsally flattened fish of uniformly dark brownish coloration and a relatively high dorsal fin with seven branched rays, known only from the rapids of the rivière Ngounié (Ogowé basin) near Lebamba, Gabon.

Gymnallabes Günther 1867

Type species: *Gymnallabes typus* Günther, 1867:111.

This genus was diagnosed by Boulenger (1911:270) as a "degraded, anguilliform *Clarias*, with the sides of the head unprotected by bone, even the postorbital shield being absent, the pectoral and ventral fins very small, no free border to the eye, and the dorsal and anal completely united with the caudal."

Gymnallabes typus is known from the southern parts of Nigeria and Dahomey (Daget and Iltis, 1965:168) but the kind of habitat is unrecorded. *G. alvarezi* Roman (1971:112–113, fig. 46), a very similar species, was based on a single specimen from the Río Kie, a tributary of the Río Ntem or Campo, near Ebebiyin in Guinea Ecuatorial. *G. tihoni* Poll 1944, the only other species referred to the genus, was described from rapids habitats near Kinsuka. The anatomy of this cryptophthalmic and remarkably flattened species has not been adequately compared with that of *typus*. Our colleague, Prof. Max Poll, has indicated that it may represent a new genus, a problem he is studying. Our rapids collections include numerous specimens of *tihoni*, and a single specimen of a closely related species which is completely depigmented and entirely without eyes. Pending the results of Prof. Poll's study we place this new species in *Gymnallabes*.

Gymnallabes nops new species
Plates 7, e and 8, a

Holotype. MCZ 50298, 57.0 mm, R & S 35.

Diagnosis. *G. nops* is closely related to *tihoni*, from which it differs most strikingly in being completely eyeless and depigmented. In *nops* the pectoral fins do not reach the dorsal fin origin, and the pelvics do not reach the anal origin, while in *tihoni* the pectorals and pelvics extend beyond the origins of these fins. In *nops* the innermost pelvic ray is longer than the outermost, while in *tihoni* it is extremely reduced. *G. nops* has more gill rakers, fewer rays in the dorsal and anal fins, and more precaudal vertebrae but fewer total vertebrae than *tihoni*. The body at the dorsal fin origin and the caudal peduncle are deeper in *nops* than in *tihoni*, and the pectoral spine is shorter; the distance from occipital

Table 13. Proportional measurements and counts in *Gymnallabes tihoni* and *nops*.

	tihoni	*nops*
n: S. L. mm	5: 75.2–173.6	1: 57.0
Snout-occipital crest	11.3–14.3	13.9
Occipital crest-dorsal fin origin	4.0–6.25	11.1
Snout-anus	25.1–30.3	39.6
Body depth	5.40–6.86	8.77
Caudal peduncle depth	1.90–2.18	3.85
Pectoral fin	6.80–8.73	9.47
Pectoral spine	5.07–6.13	3.50
Dorsal fin rays	122 (n = 1)	75
Gill rakers on first arch	10–11	15
Precaudal postweberian vertebrae	10–11	15
Total postweb. vertebrae	67–73	57

bone to dorsal fin origin is almost twice as great in *nops*. The mandibular muscles extend further dorsally onto the head, leaving a narrower exposed cranial surface than in *tihoni* (compare the dorsal views in Plate 7).

Counts and measurements of *nops* and *tihoni* are presented in Table 13.

Comments. If our assumption that *nops* is an anophthalmic species is correct, then it is the only such species known from the Zaire rapids as all of the other fishes with reduced eyes are either microphthalmic or cryptophthalmic. Our only specimen was the lone *Gymnallabes* taken in a relatively quiet, silted backwater open to the mainstream. Of 168 *tihoni* in our collections, only one has the eyes missing, a 75-mm specimen from R & S 41. This eyeless individual has normal pigmentation, and agrees with *tihoni* in all counts and measurements; it has 11 postweberian precaudal vertebrae and a total of 67 or 68 postweberian vertebrae. Eyeless individuals have been reported in other species of Clariidae. David and Poll (1937:234) reported two eyeless individuals of the normally microphthalmic *Channalabes apus* among a sample of 68 specimens from Kunungu. (This species inhabits forest streams and swamps, sometimes burrowing into the masses of tree roots underneath overhanging banks.)

Atopochilus Sauvage 1878

Type species: *Atopochilus savorgnani* Sauvage 1878, by original designation.

Mochokids with lips forming an expanded oral disc. Premaxillary teeth in two series: an external series with spatulate crowns on the anterior portion of the oral disc, outside the buccal cavity, which works directly against the substrate; and an internal series with needlelike crowns, at the entrance to the buccal cavity, which works against the mandibular tooth series. Mandibular tooth series consisting of a single row of tooth families, increasing in number with age, and with six to eight teeth in each fully-formed tooth family; mandibular teeth with bifid crowns in young, crowns bifid in adults of some species, but becoming spatulate in adults of other species (no other mochokids develop bifid teeth).

Confined to the Zaire basin except for one apparently endemic species in the Ogowé basin and another in one or two coastal river basins in Tanzania, *Atopochilus* includes 13 nominal species (Poll, 1959: 106–107). Unfortunately, most descriptions have been based on one or a few specimens only, often either very small juveniles or the largest size of adult, and no attempt has been made to account for growth changes within species, which are considerable. Some grow to half a meter or more in standard length, and undergo sub-

→

Plate 7

a–c. *Notoglanidium pallidum* new species, holotype, 53.6 mm. Zaire River at Bulu (MCZ 50236).
d. *Gymnallabes tihoni*, 75 mm. Zaire River at Tadi (MCZ 50297).
e. *Gymnallabes nops* new species, holotype, 57.0 mm. Zaire River at Tadi (MCZ 50298).

Plate 7

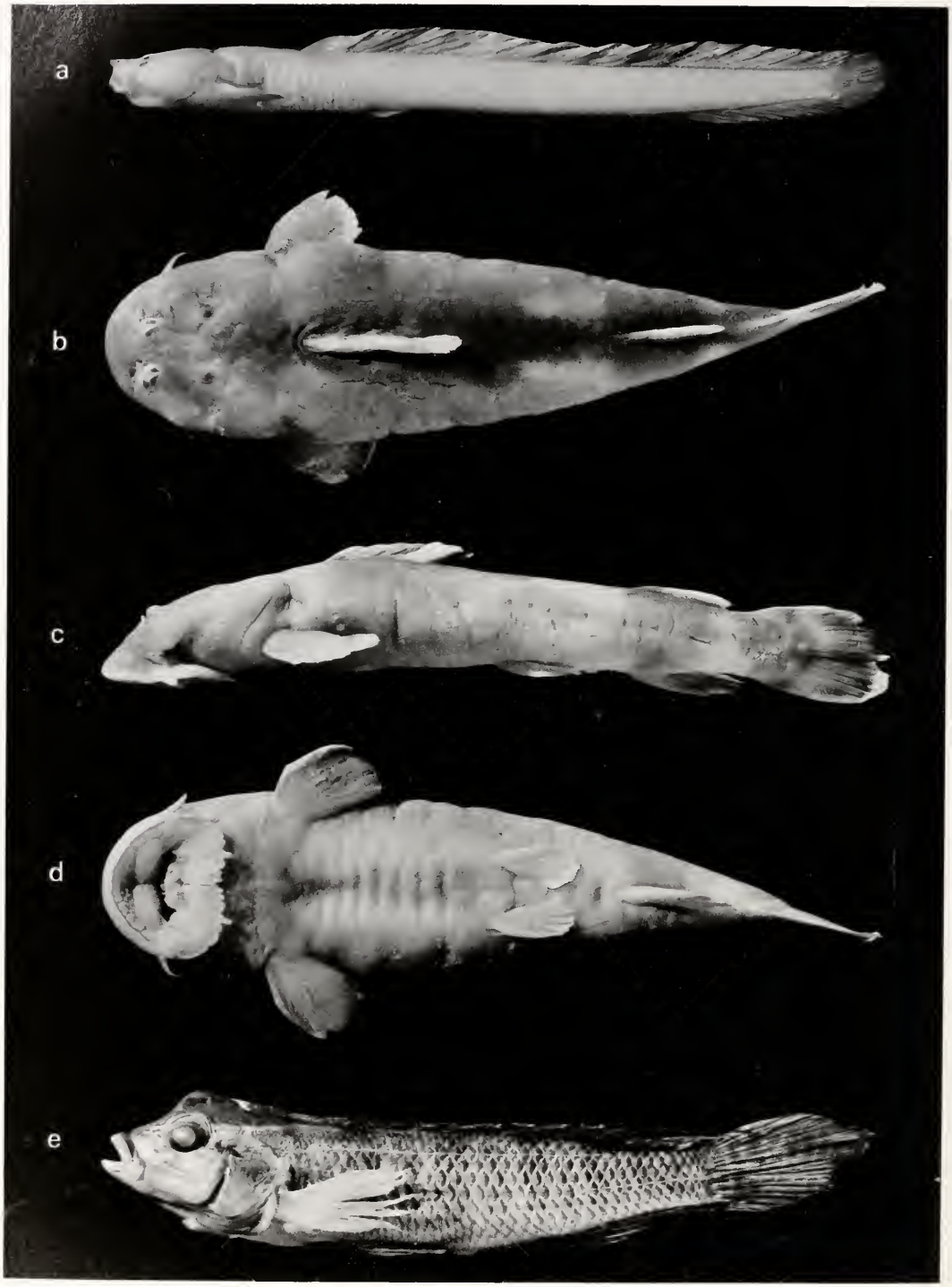

Plate 8

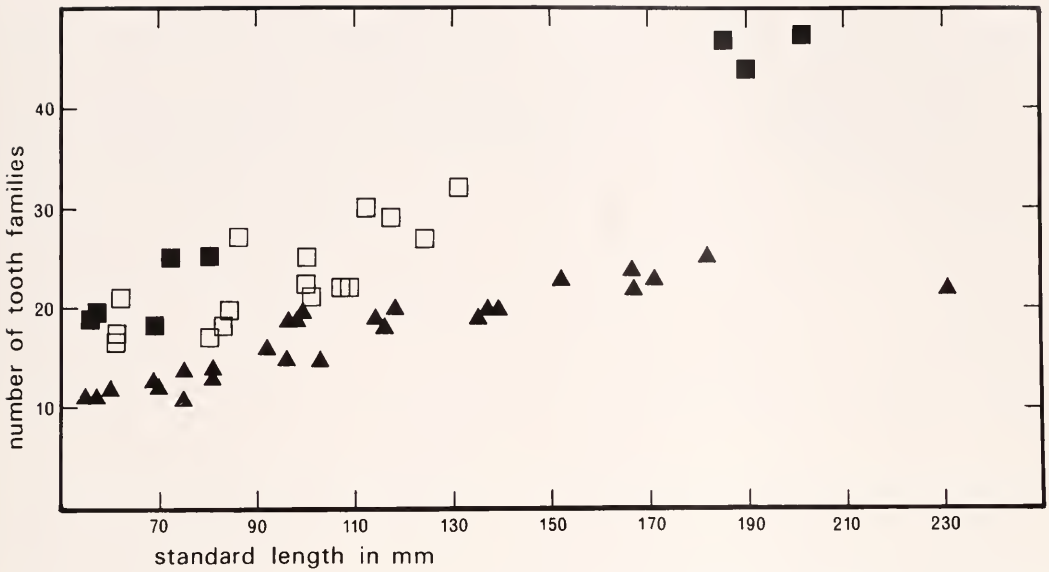

Figure 4. *Atopochilus*. Number of mandibular tooth families plotted against standard length. ▲ *guentheri*, Lower Zaire R. (MCZ 50147, 50194, 50300, 50381, 50463 and 50538); ■ *royauxi*, Lower Zaire R. (MCZ 47989, 50148 and 50539); □ *royauxi*, Ubangui (MCZ 48357 and 48358).

stantial allometry. There are also ontogenetic changes in dentition (Poll, 1967:258–263). The genus is badly in need of taxonomic revision, but this should be deferred until sufficient material has been collected to permit study of growth changes and other variation.

Body form varies greatly within the genus, from short, stocky species to elongate and greatly depressed ones. Our rapids collections include two species, *A. guentheri* and *A. royauxi*, in both of which adults have elongate and greatly depressed bodies. They are superficially very similar, and thus it is of interest that we found them sympatric at two localities. There are slight differences in coloration and in several proportional measurements (Table 14), but the surest way to distinguish them is by counting the mandibular tooth families. These range from 11 or 12 to 25 in *A. guentheri* of 57–230 mm, and from 18 or 19 to 47 in *A. royauxi* of 54–201 mm, and are always more numerous in *A. royauxi* at any given standard length. The number of mandibular tooth families in the two species is plotted against standard length in Figure 4. The data for *A. royauxi* include material from Ubangui. It is interesting to note that specimens from Ubangui may not differ from *A. guentheri* as sharply as do those from the Lower Zaire River. This is possibly an example of character displacement: *A. guentheri* has not been reported from Ubangui. The dentition of a 58-mm *A. guentheri* with 12 mandibular tooth families is illustrated in Figure 5. Additional mandibular tooth families are apparently formed near the symphysis of the mandible as well as at the outer ends of

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Plate 8

a. *Gymnallabes nops* new species, holotype, 57.0 mm. Zaire River at Tadi (MCZ 50298).
b–d. *Chiloglanis carnosus* new species, holotype, 54.1 mm. Zaire River at Inga (MCZ 50464).
e. *Lamprologus werneri*, 62 mm. Zaire River at Kinganga (MCZ 50390).

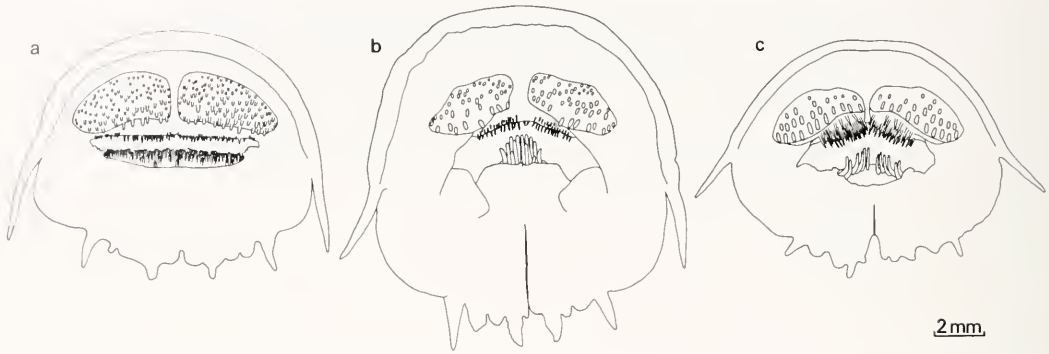

Figure 5. Mochokidae, oral disc and dentition: a. *Atopochilus guentheri*, 58 mm; b. *Chiloglanis congicus*, 60 mm; c. *Chiloglanis carnosus*, 61 mm.

the mandibular tooth row. Our counts exclude partially formed tooth families near the symphysis in which none of the teeth lies as far forward as the anteriormost teeth of previously formed tooth families. The histology of the tooth families and the mode of tooth replacement have not been studied. We suspect that within each tooth family, the anteriormost teeth are the first to be discarded and are successively replaced by the more posterior ones, which continuously "migrate" forward.

Table 14. Differences between two species of *Atopochilus* from the Lower Zaire River.

	guentheri	*royauxi*
Standard length mm	57–230	54–201
Head	27.4–30.2	28.7–31.7
Eye	2.0– 3.4	2.7– 4.9
Oral disc length	15.8–20.9	17.6–20.0
Oral disc width	21.0–24.5	24.6–26.4
Mandibular tooth pad length	11.3–13.4	13.4–16.6
External premaxillary tooth pad width	6.7– 8.4	8.5– 9.7
Dorsal spine length	6.3–10.4	8.9–11.5
Body depth	12.9–16.4	14.2–18.2
Spots on abdomen	absent	often present
Number of mandibular tooth families	11–25	18–47

Chiloglanis Peters 1868

Type species: *Chiloglanis deckenii* Peters 1868.

A rheophilic genus of small to moderately large mochokids with a sucker mouth, closely related to *Atopochilus*, but distinguished from that genus by having mandibular teeth far fewer and unicuspid throughout life (Figure 5). A description of the dentition is given by Trewavas (1974:358–359). See also our remarks under *Atopochilus*. Our rapids collections include two species of *Chiloglanis*, one undescribed.

Chiloglanis carnosus new species
Plate 8, b–d

Holotype. MCZ 50464, 54.7 mm, R & S 38.
Paratypes. MCZ 50465, 15: 23.8–58.0 mm, R & S 38; MCZ 50541, 27: 19.9–61.0 mm, R & S 41; MCZ 50301, 1: 32.2 mm, R & S 35; MCZ 50382, 7: 31.8–47.3 mm, R & S 28; MCZ 50241, 21: 21.2–57.7 mm, R & S 29.

Diagnosis. Distinguished from all previously described *Chiloglanis* by its short, flat body (width of body divided by depth 1.4–2.1), and furthermore in having a low dorsal fin. Head smooth, without tubercles; diameter of eye 1.6–2.6; fewer than 30 teeth on main tooth-bearing area of each premaxillary; gill opening restricted, terminating well above pectoral spine, its length

Table 15. Proportional measurements in *Chiloglanis congicus* and *C. carnosus* (n = 10).

	congicus	*carnosus*
Standard length	48.7–65.1 mm	38.5–60.1 mm
Body width	20.5–22.0	23.2–30.2
Body depth	16.2–18.4	13.2–19.6
Head length	35.3–37.1	28.0–32.4
Head width	24.3–25.1	23.2–29.3
Oral disc length	22.6–24.9	16.9–19.5
Oral disc width	20.1–25.0	19.6–23.9
Maxillary barbel	6.0– 7.2	4.1– 6.8
Outer mandibulary barbel	4.1– 4.7	1.4– 2.2
Snout	22.9–24.2	18.1–22.9
Eye	2.6– 3.3	1.6– 2.5
Interorbital space	7.7– 8.7	5.6– 9.0
Gill opening	8.2– 9.2	3.9– 4.6
Predorsal length	40.2–42.7	33.9–38.2
Last dorsal ray to adipose	13.0–16.2	27.4–31.8
Dorsal spine	8.1–10.1	3.7– 5.8
Dorsal fin height	13.5–15.9	8.9–12.4
Adipose fin length	21.7–23.7	10.7–14.0
Adipose fin height	3.9– 4.7	2.2– 2.8
Pectoral spine	10.8–14.1	7.4– 9.9
Pectoral fin	19.0–22.1	15.5–19.5
Pelvic fin	13.3–15.7	11.0–14.0
Caudal peduncle length	14.8–17.4	12.9–15.6
Caudal peduncle height	8.4– 9.4	8.5–10.5

3.9–4.6; complete vertebral centra behind fused Weberian vertebrae only 24 or 25 (usually 24); back and sides dark blue or bluish grey, with pairs of oval, cream-colored marks anterior and posterior to adipose fin, entire ventral surface of head and body cream-colored or whitish.

Proportional measurements are presented in Table 15.

Dentition (Figure 5). In seven specimens 44–60 mm S. L., the number of teeth on the main tooth-bearing area of the premaxillary varies from 22 to 27, with no relation to length of specimens. There are about 33–35 teeth on the secondary tooth-bearing area of the premaxillary (the small teeth which oppose the dentary teeth), except in one specimen with only 23. The dentaries bear either a single row of teeth, or two rows, in which case the inner row consists of replacement teeth that have just erupted or have yet to erupt from the epidermis overlying them. The number of teeth in the outer tooth row of each dentary varies from five to seven.

Comments. In addition to *C. carnosus,* our rapids collections include specimens which correspond to the description and figures of *C. congicus* Boulenger 1920. The *congicus* differ strikingly from *carnosus* by their higher body (width of body divided by depth 1.1–1.3), higher dorsal fin, larger oral disc, longer barbels, more numerous teeth on main tooth-bearing portion of premaxillary (47–62 teeth on each premaxillary in specimens from 49–87 mm S. L., number of teeth increasing with length of specimens), gill opening extending anteroventrally to in front of pectoral spine insertion, complete vertebral centra behind fused Weberian vertebrae 26–28 (usually 27), and brownish grey back and sides. There are numerous differences in proportional measurements between *carnosus* and *congicus* (Table 15). The dentition of *congicus* is illustrated in Figure 5.

Lamprologus Schilthuis 1891

Type species: *Lamprologus congoensis* Schilthuis, 1891:85–86, pl. 6, fig. 1.

This genus, endemic to the Zaire basin, differs from most other African cichlids in having 4–10 spines in the anal fin, and upper and lower jaws with bands of fine unicuspid teeth and 6–10 enlarged canines anteriorly; scales ctenoid. Pharyngeal apophysis formed by basioccipital bones as well as parasphenoid. Three riverine species are currently recognized: *L. congoensis, L. moquardii* Pellegrin 1903, and *L. werneri* Poll 1959. Our rapids collections include many *werneri* (two color varieties?), a small series perhaps identical with *moquardii,* and two specimens of an un-

TABLE 16. MORPHOMETRIC AND MERISTIC CHARACTERS OF *LAMPROLOGUS LETHOPS*.

	Holotype	Paratype
S. L. mm	27.0	87.9
Head length	30.4	24.9
Head width	20.0	22.5
Body depth	17.8	16.7
Body width	17.0	17.5
Last dorsal spine	9.3	8.0
Last anal spine	10.0	8.3
Pectoral fin	23.0	28.8
Pelvic fin	20.0	16.4
Caud. ped. length	13.7	13.7
Caud. ped. height	10.7	11.4
Dorsal spines	20	20
Dorsal rays	7	7
Anal spines	6	7
Anal rays	6	5
Lateral line scales	45	50
Upper pored scales	30	41
Lower pored scales	12	23
Circumped. scales	24	25
Upper/lower canines	6/8	6/6
Gill rakers	11 + 1 + 4	—
Vertebrae	—	15 or 16 + 17

described species which differs from all other known cichlids in being cryptophthalmic and depigmented.

Lamprologus lethops new species
Plate 9, a–c

Holotype. MCZ 50248, 27.0 mm, R & S 29.
Paratype. MCZ 50249, 87.9 mm, R & S 29.

Diagnosis. A cryptophthalmic, depigmented *Lamprologus* with a relatively flat head and nearly cylindrical body. It is further distinguished from all other riverine *Lamprologus* by its relatively small scales.

Counts and measurements of the two type specimens are given in Table 16. There are two or three suborbitals, the lacrimal with two enlarged lateralis canals extending to its lower rim and one or two small suborbitals (variable). A line of small neuromasts extends posterodorsally on the skin from the last suborbital to the anterior lateralis pore on the pterotic bone, as in most other *Lamprologus*. The basioccipital is incorporated into the pharyngeal apophysis as in other *Lamprologus*. The pharyngeal teeth are moderately molarized (Figure 6).

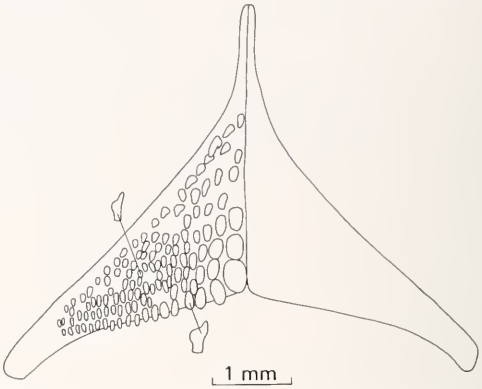

Figure 6. *Lamprologus lethops*, 88 mm, pharyngeal dentition.

Comment. In generic characters, *lethops* agrees fully with the type species of *Lamprologus*.

Nanochromis Pellegrin 1904

Type species: *Pseudoplesiops nudiceps* Boulenger 1899, by original designation.

Nanochromis sensu stricto is distinguished from other African cichlids by having one half or more of the upper row of scales bearing lateral line tubules adjacent to the base of the dorsal fin, rather than separated from it by one or more rows of scales without tubules. The group thus defined includes all of the species dealt with here.

→

Plate 9

a. *Lamprologus lethops* new species, holotype, 27.0 mm. Zaire River at Bulu (MCZ 50248).
b–c. *Lamprologus lethops* new species, paratype, 87.9 mm. Zaire River at Bulu (MCZ 50249).
d. *Nanochromis nudiceps*, lectotype, 48.5 mm. Kutu, Zaire (RGMC 1045).
e. *Nanochromis* sp. undet., 45 mm. Small stream near Boende, Cuvette Centrale, Zaire (MCZ 48004).

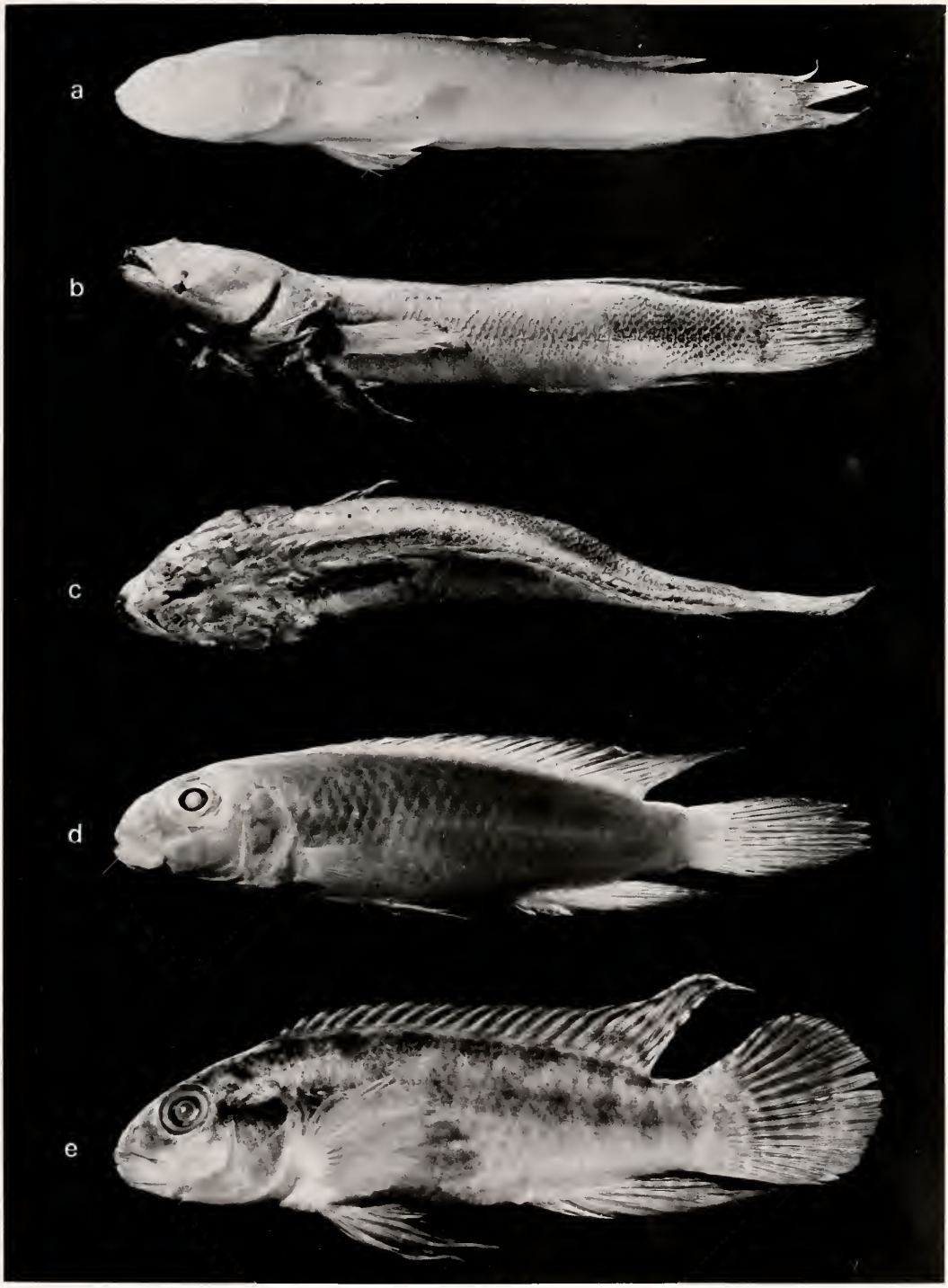

Plate 9

Thys (1968) and Thys and Loiselle (1971) have broadened the generic concept to include several species from Upper Guinea and Lower Guinea, but this does not concern us in the present context.

There are three nominal species of *Nanochromis sensu stricto: N. nudiceps, dimidiatus,* and *squamiceps.* Our rapids collections include four new species which are clearly distinct from *dimidiatus* and *squamiceps.* A problem arises with *nudiceps,* however, because the type series is polytypic. We examined two of the four syntypes and found they belong to different species. It is necessary to designate a lectotype before describing our new species.

Table 17. Frequency of total dorsal elements in species of *Nanochromis* (total dorsal elements = number of spines plus rays in dorsal fin, last ray counted as one when split to base).

		22	23	24	25	26	27
nudiceps	Kutu					1	
sp. undet.	Boende			1		1	
	Bandundu			1		2	
consortus	Inga				6		
parilus	Wombe					6	4
	Kinganga					10	
	Inga				2	7	1
minor	Tadi		1				
	Kinganga	1	1	1			
splendens	Tadi			9	1		
	Kinganga		1	8	1		
	Inga		2	6	2		

Nanochromis nudiceps (Boulenger) 1899
Plate 9, d

Lectotype. RGMC 1045, 48.5 mm, Kutu, Cuvette Centrale. M. P. Delhez, 1899.

Diagnosis. A relatively large *Nanochromis* with level dorsal profile; about last 10 dorsal spines subequal in length; nape scaleless; caudal peduncle as long as high; entire caudal fin with rows of small dark spots forming six to eight narrow vertical bars; soft-rayed portions of dorsal and anal fins with bars similar to those on caudal; dorsal and caudal fins without a dark margin or light submargin.

Counts and measurements are given in Tables 17 and 18.

Comments. Boulenger's description of *nudiceps* is based on all four syntypes, but the one we have selected as lectotype is the largest and best preserved of the four, and the one selected by Boulenger to serve as the figure for his new species. The other three syntypes, all from Stanley Pool (= Malebo Pool), are small and in poor condition; they differ from the lectotype in having a black margin and light submargin on the dorsal fin and upper edge of the caudal fin. Such coloration distinguishes one of our new species, *N. parilus,* with which they may be identical.

The four new species about to be described agree with *nudiceps* as well as sp. undet. in having only two infraorbital bones, a lacrimal with two lateralis canals extending to its lower rim, and an elongate second infraorbital. The posterior end of the second infraorbital tends to project straight back, rather than follow the orbital rim. The new species further agree with *nudiceps* but differ from sp. undet. in lacking predorsal bones and in having five lateralis pores on the mandible and seven on the preopercle (including one at the junction with the skull). *N.* sp. undet. has one predorsal bone, four mandibular pores and six preopercular pores. The new species all have scaleless cheeks, and three of them also have scaleless napes, as in *nudiceps.* One new species, *consortus,* has scales on the nape, but they are minute and few in number. *N. dimidiatus* and *squamiceps,* on the other hand, have large scales on the cheeks and on the nape.

Apart from *nudiceps,* the only previously described *Nanochromis sensu stricto* are *N. dimidiatus* (Pellegrin) 1900 (type locality Banghi) and *N. squamiceps* (Boulenger) 1902 (type locality Lindi River, Upper Congo). Matthes (1964:134–137) placed *squamiceps* in the synonymy of *dimidiatus*; Thys (1968:387) indicated they

are distinct but did not record his observations. *N. dimidiatus* differs from *nudiceps*, and from all of our new species, in having one or two moderately large scales just below the posterior portion of the eye (at least in some specimens), and a dark longitudinal band extending midlaterally from the posterior edge of the eye to the end of the caudal fin (see Pellegrin, 1904, pl. 4, fig. 2). Two specimens from Bangui in the British Museum (BMNH 1975.2.10: 1–2) agree with the description of *dimidiatus*, and are distinct from our new species; we have not examined the type specimens. The relatively deep-bodied specimens from Boende and Bandundu in the Cuvette Centrale, reported here as *Nanochromis* sp. undet. (Tables 17–18, Plate 9e), may represent a new species: we had originally identified them as *dimidiatus*. *N. squamiceps* differs from *nudiceps* and from all our new species in having large scales on the nape and cheek. *N. dimidiatus* and *squamiceps* further differ from all of our new species in having the caudal fin uniformly marked with rows of small dark spots forming several narrow vertical bars (as in *nudiceps*).

Nanochromis consortus new species
Plate 10, a, b

Holotype. MCZ 50551, 52.2 mm, R & S 41.
Paratypes. MCZ 50552, 5: 26.0–49.0, R & S 41.

Diagnosis. A *Nanochromis* with dorsal fin spines stubby anteriorly, increasing regularly in length from first to last; total dorsal elements modally 25 (Table 17); nape with a few small, embedded scales; mature females with anterior half of anal fin black.

This species differs strikingly from *dimidiatus* and *minor*. It is readily distinguished from *splendens* by coloration and morphometric characters (Table 18). It is similar in meristics to *parilus* and *nudiceps*. From *parilus* it differs in coloration, in the profile of the spinous dorsal fin, and in adults having a smaller eye (eye diameter 27.6–31.8% of head length in *consortus* versus 29.4–33.0% in *parilus*). It differs from *nudiceps* in the coloration of the caudal fin, in the profile of the spinous dorsal fin, and in the ratio of caudal peduncle length to height (Table 18).

Size. Our two largest *consortus*, 49.0– and 52.2-mm males, are about 4–7 mm longer than the largest *splendens* and 5–8 mm longer than the largest *parilus* we obtained. The largest female is 40.7 mm.

Coloration. Life colors unrecorded. Preserved specimens of both sexes, adults as well as young, have body beige with grey edgings on scales, and no trace of vertical bars. Forehead, nape, and lacrimal rusty brown, apparently due to underlying adipose tissue. Sexually mature males and females differ in the coloration of the fins, all of which except the pectoral fin tend to be longer in males. In males posterior portion of soft dorsal and upper two-thirds of caudal with several vertical rows of dark spots; upper third of caudal sometimes with longitudinal streaks between the rays and lower third of caudal dusky, without marks, indicating that in life the upper half of the caudal differs in color from the lower half; anterior two-thirds of anal dusky, posterior third yellowish near base with faint indication of vertical bars. In females, dorsal, caudal, and posterior half of anal fins plain, dusky grey. The only mature female in our collection, which is gravid, has the anterior half of the anal fin black (Plate 10, b), a feature not found in any other *Nanochromis* of either sex.

Nanochromis parilus new species
Plate 10, c, d

Holotype. MCZ 50474, 44.1 mm, R & S 38.
Paratypes. MCZ 50475, 38: 21.6–41.4 mm, R & S 38; MCZ 50202, 11: 11.5–40.8 mm, R & S 19; MCZ 50250, 1: 30.8 mm, R & S 29; MCZ 50309, 3: 31.8–42.1 mm, R & S 35; MCZ 50340, 14: 13.4–44.1 mm, R & S 26; MCZ 50391, 5: 19.3–41.5 mm, R & S 28.

Diagnosis. *N. parilus* differs from all other *Nanochromis sensu stricto* in having

TABLE 18. MORPHOMETRIC AND MERISTIC CHARACTERS IN *NANOCHROMIS SENSU STRICTO*.

	nudiceps[1]	sp. undet.[2]	*consortus*[3]	*parilus*[4]	*minor*[5]	*splendens*[6]
n: S. L. mm	1: 48.8	5: 29.2–45.0	6: 26.0–52.2	10: 32.4–44.1	4: 21.0–23.8	10: 33.3–43.2
Head	31.6	32.6–34.7	29.6–33.1	30.7–34.3	32.3–34.5	31.0–35.0
Eye (% headlength)	31.2	28.3–30.9	27.6–31.8	29.4–33.0	29.3–30.0	28.7–34.5
Interorbital (% headlength)	16.2	21.6–23.6	16.1–18.2	12.8–16.5	17.9–19.5	12.1–15.6
Preorbital (% headlength)	18.8	9.9–15.7	14.8–19.2	13.6–17.7	11.4–12.2	15.2–19.4
Depth	24.8	28.4–30.9	23.8–25.1	23.3–27.8	23.6–26.1	20.4–24.9
Last dorsal spine	14.6	10.0–14.2	11.8–15.1	12.2–15.9	15.2–16.8	11.2–16.0
Pectoral fin	23.0	23.8–27.3	19.7–23.8	22.7–25.8	19.3–21.9	21.3–22.9
Pelvic fin ♂	30.5	—	28.5–29.8	26.3–33.9	25.6–32.2	35.4–43.0
Length caudal ped./height caudal ped.	0.98	0.90–1.00	1.25–1.42	1.09–1.32	0.97–1.22	1.17–1.38
Dorsal spines	18	17–19	18	18–19	17–18	16–18
Dorsal rays	8	7–8	7	7–8	5–6	6–7
Anal rays	6	5–6	5–6	6–7	5–6	6
Upper pored scales	14	8–11	8–13	11–16	6–10	11–16
Lower pored scales	4	2–4	2–6	3–7	2–5	4–6
Midlateral scales	26	24–25	26–28	25–27	23–24	25–27
Transverse scales[7]	9	7–8	9–10	9	7	8–10
Gill rakers	8+1+3	7–9+1+3–4	7–9+1+3–4	7–9+1+3–6	6+1+2–3	7–9+1+3–6
Vertebrae	27	25–26	28 (n = 3)	27–29	25	27–28

[1] RGMC 1045 (lectotype). [2] MCZ 48004, Boende; MCZ 50588, Bandundu. [3] MCZ 50551 (holotype); MCZ 50552 (paratypes). [4] MCZ 50474 (holotype); MCZ 50475 (paratypes). [5] MCZ 50341 (holotype); MCZ 50342 (paratypes). [6] MCZ 50476 (holotype); MCZ 50477 (paratypes). [7] Number of scales in an oblique row extending dorso-anteriorly from base of third anal spine to base of dorsal fin.

a black margin and light submargin on the dorsal fin and upper edge of the caudal fin, and no vertical markings on the caudal fin in either sex. It differs from sp. undet., *consortus,* and *minor* in having the last ten spines in the dorsal fin subequal in length, and differs from other *Nanochromis* except *nudiceps* in having a mode of 26 total dorsal elements (Table 17). Sexual dichromatism is slight compared to other species from the Lower Zaire rapids.

Counts and measurements are given in Table 18.

Size. Our largest male is 44.1 mm. The largest female is 40.8 mm; a gravid specimen with about 100 eggs up to .5 mm in diameter is 34.4 mm.

Color. In both sexes, dorsal portions of head and body olivaceous; cheek blue; ventral portion of branchiostegal membranes reddish; eye with a rusty-red spot on upper orbital rim and a dark iris; body behind pectoral fin with an iridescent blue-green patch grading into a rosy-violet patch posteriorly which extends onto belly; dorsal fin and upper portion of caudal fin with a black margin and light submargin; light submargin on caudal yellow-orange and bordered by a dark streak ventrally; lower half of caudal and entire anal fin violet, without distinct marks; pelvic fins whitish with grey outer rays. In mature females, violet patch on belly tends to be more intense than in males; and outer rays perhaps less dusky. No other sexual differences in coloration observed.

Comments. Nanochromis from Malebo Pool identified as *nudiceps* by Poll (1939: 44, fig. 25) agree with *parilus* in having a black margin on the dorsal fin and upper edge of the caudal. They differ primarily in having small round spots arranged in seven vertical bars on the lower half of the caudal fin, as in *splendens.* At five localities in the rapids we obtained from one to four specimens resembling Poll's Malebo Pool material, always in the presence of larger numbers of *parilus,* and, except at one locality, larger numbers of *splendens* (Table 3). These undetermined *Nanochromis* may be sexually dichromatic *parilus,* hybrids between *parilus* and *splendens,* or possibly yet another species. We are inclined to feel that the first of these three hypotheses offers the most likely explanation.

Nanochromis minor new species
Plates 10, e; 11, a

Holotype. MCZ 50341, 23.3 mm, R & S 26.
Paratypes. MCZ 50342, 2: 21.0–22.5 mm, R & S 26; MCZ 50310, 1: 23.8 mm, R & S 35.

Diagnosis. N. minor differs from all other known African cichlids in its tiny adult size and in having sharp points on the posterior edge of the opercle and subopercle. It further differs from all other *Nanochromis* in having a black-tipped mandible and sharply defined, lunate brown (or maroon) marks on the scales. The numbers of gill rakers, of vertebrae, of scales, and of total dorsal elements are fewer than in any other *Nanochromis* (Tables 17 and 18). Dorsal spines short anteriorly, increasing regularly in length from first to last, in contrast to all other *Nanochromis* except sp. undet. and *consortus.*

Size. Our three males, 22.5–23.8 mm, all have well-developed sexually dimorphic coloration. The one female, a gravid specimen with roughly 40 eggs .3 mm in diameter, is 21.0 mm.

Color. In both sexes, tip of mandible black and scales with sharply defined, lunate brown or maroon marks; eye with a rusty-red spot on upper orbital rim and a white iris. In males, branchiostegal membranes and adjacent breast reddish; dorsal and anal fins with dark brown vertical marks; upper third of caudal yellowish, lower two-thirds with large roundish brown spots arranged in five or six vertical bars on a clear background; a longitudinal band extends from the head to the base of the caudal fin, where it stops. In females, body behind pectoral fin with a violet patch extending onto the belly; longitudinal band

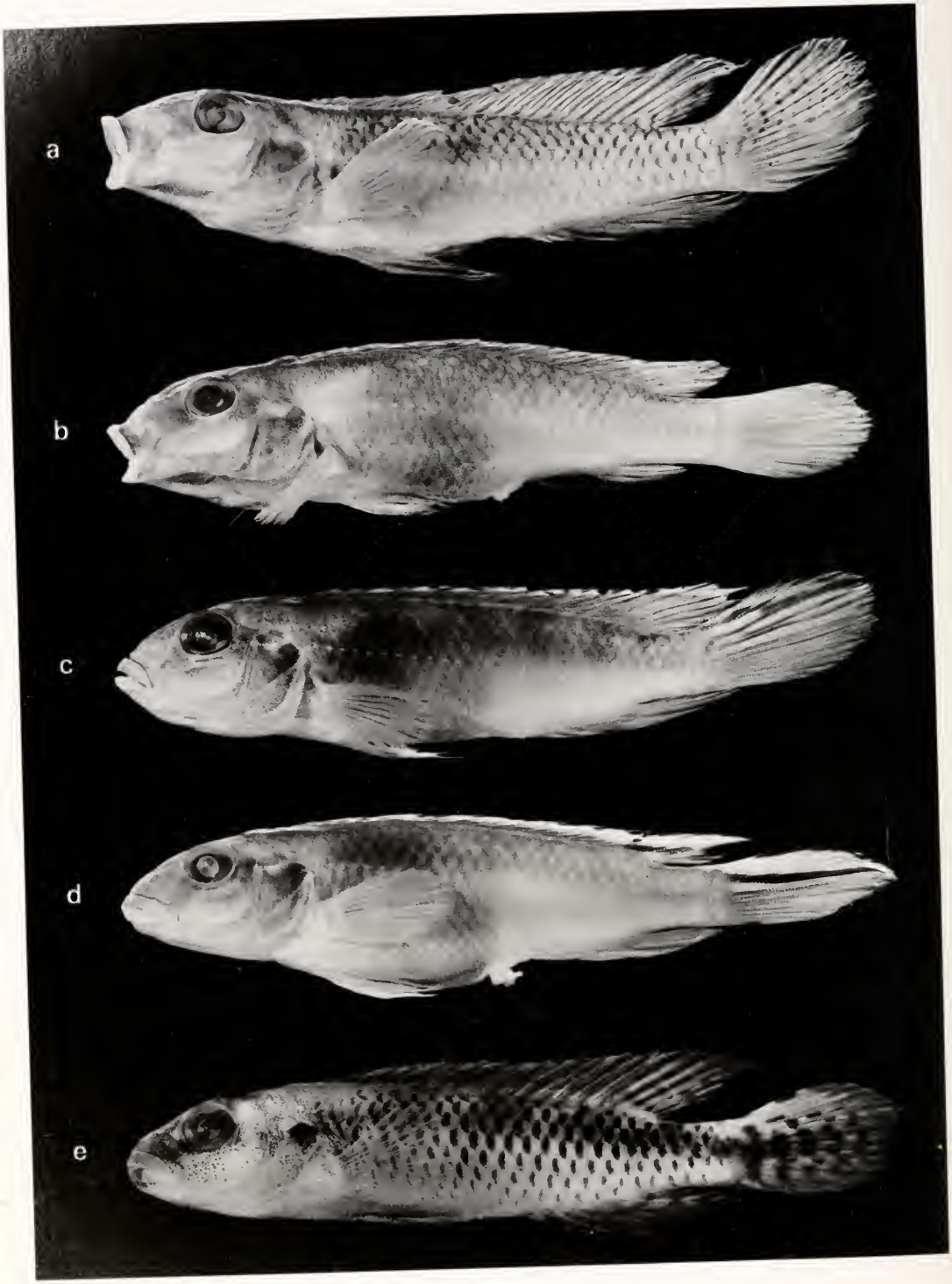

Plate 10

from head to base of caudal fin continued to end of middle caudal fin rays; upper and lower portion of caudal fin each with a maroon band paralleling the longitudinal band on middle of caudal fin, rest of caudal fin clear; dorsal and anal fins dusky brown, without markings.

Comment. *N. minor* were found only in relatively still backwaters, open to the mainstream, with mixed rock and silty-sand bottom, where the only other fishes were also small and few in number.

Nanochromis splendens new species
Plate 11, b, c

Holotype. MCZ 50476, 43.1 mm, R & S 38.
Paratypes. MCZ 50477, 170: 16.4–45.3 mm, R & S 38; MCZ 50311, 61: 13.2–44.6 mm, R & S 35; MCZ 50343, 5: 9.0–34.0 mm, R & S 26; MCZ 50392, 87: 14.2–42.0 mm, R & S 28; MCZ 50553, 28: 15.4–42.8 mm, R & S 41.

Diagnosis. A slender *Nanochromis* differing from all others in having canary yellow and orangish red pigments on the gill covers of both sexes at maturity; males with long, filamentous black pelvic fins and vertical carmine bars on lower half of caudal fin; body depth of males 20.4–22.0% S. L. (versus 23.3–30.9% in all other species). *N. splendens* differs from sp. undet., *consortus*, and *minor* in having the last 10 dorsal spines subequal in length; it differs from *nudiceps* and from the other species collected in the Lower Zaire rapids in having a mode of 24 total dorsal elements (Table 17).

Counts and measurements are presented in Table 18.

Size. Our largest male is 45.3 mm. The largest female is 36.9 mm; a gravid specimen with about 50 eggs 1.2–1.8 mm in diameter is only 30.0 mm.

Color. In both sexes, dorsal portions of head and body olivaceous; gill covers canary yellow anteriorly and orangish red posteriorly; eye with a red spot on upper orbital rim; iris white, making the eye appear larger than it would otherwise; scales on body with faint grey edges; body with five or six indistinct vertical bars, and an iridescent blue patch behind the gill cover grading to dark bluish violet behind the pectoral fin.

In males, cheek iridescent blue; branchiostegal membranes red; dorsal fin yellowish, with brown streaks paralleling the spines and rays; tips of dorsal spines with yellow lappets; soft portion of dorsal with dark grey margin extending to upper edge of caudal fin; upper half of caudal yellowish orange, with horizontal brown streaks, lower half with seven to eight vertical carmine bars on a clear background; posterior half of anal fin similar to lower half of caudal, anterior half of anal carmine on base and dark grey distally; filamentous outer ray of pelvic fin black, inner rays whitish.

In females, cheek canary yellow; branchiostegal membranes dusky yellowish; belly and vent region violet; spinous portion of dorsal fin red-orange along the base, grading to yellow distally; caudal yellowish at base grading to reddish distally, without distinct marks; anal uniformly bluish; outer pelvic rays white, inner rays clear. In 10–30% of the females, including specimens as small as 9 mm, the soft-rayed portion of the dorsal fin has a large black spot partially surrounded by lightened areas (Plate 11, c). Such a distinctive spot is not found in either sex of any other *Nanochromis*.

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Plate 10

a. *Nanochromis consortus* new species, holotype, ♂, 52.2 mm. Zaire River at Inga (MCZ 50551).
b. *Nanochromis consortus* new species, paratype, ♀, 40.7 mm. Zaire River at Inga (MCZ 50552).
c. *Nanochromis parilus* new species, holotype, ♂, 44.1 mm. Zaire River at Inga (MCZ 50474).
d. *Nanochromis parilus* new species, paratype, ♀, 40.8 mm. Zaire River near Wombe (MCZ 50202).
e. *Nanochromis minor* new species, holotype, ♂, 23.3 mm. Zaire River near Kinganga (MCZ 50341).

In juveniles the vertical bars on the sides of the body are more pronounced than in adults of *splendens* and juveniles of *consortus* and *parilus*.

Sexual dimorphism. In addition to the differences in size and coloration noted above, mature males of *splendens* tend to have the rays of the dorsal, anal, and pelvic fins forming filamentous extensions, and they also have a longer caudal fin than females; similar differences occur between the sexes of other *Nanochromis*, but are far less marked.

Comment. N. splendens is the most colorful and perhaps the most rheophilic *Nanochromis*.

Steatocranus Boulenger 1899

Steatocranus Boulenger, 1899:52 (type species *Steatocranus gibbiceps* Boulenger 1899, by original designation).

Leptotilapia Pellegrin 1928 (type species *Leptotilapia rouxi* Pellegrin 1928, by original designation).

Gobiochromis Poll 1939 (type species *Gobiochromis tinanti* Poll 1939, by original designation).

A rheophilic genus comprising seven closely related species endemic to the Zaire basin and one isolated species in the Volta basin, all having cycloid scales; two rows of scales bearing lateral line pores; 30–34 scales in a lateral series; 19–22 dorsal spines and three anal spines; a frontal gibbosity of variable development; and upper and lower jaws with an outer row of large bicuspid teeth and one to three inner rows of small tricuspid and conical teeth. Gill rakers on first arch 5–12. Pharyngeal apophysis formed exclusively by parasphenoid bone. Longest soft ray in pelvic fin is the third or middle ray. The species in which spawning behavior has been observed are substrate spawners, affixing their eggs to rocks. Sexual dichromatism apparently absent. Juveniles with a "tilapia-mark" on anterior base of soft-rayed dorsal fin. Vertebrae 28–31.

Our collections from the Lower Zaire rapids include four species, one of them new. In addition, we have found new species in the rivière Mbomou in Ubangui and in the rivière Mpozo, a tributary of the Lower Zaire River. Counts and measurements of all of the species of *Steatocranus* are presented in Table 19.

Steatocranus gibbiceps Boulenger 1899
Plate 11, d

Diagnosis. S. gibbiceps differs from all of its congeners in having a relatively narrow snout and upper and lower jaws with two greatly enlarged truncate teeth anteriorly (Figure 7). It differs from *casuarius* and *ubanguiensis* in coloration, and from *mpozoensis, rouxi, tinanti,* and *irvinei* in having only a single inner row of tricuspid teeth in each jaw. It is most similar to *S. glaber,* from which it differs primarily in dentition and in having a much shorter intestine.

Color. Olive brown; scales with a light-colored center and a dark submargin. Branchiostegal membrane uniformly dark brownish or blackish brown; breast cream-colored.

Comments. This is by far the most abundant species in our rapids collections. See comments under *casuarius*.

Steatocranus casuarius Poll 1939
Plate 11, e

Diagnosis. S. casuarius differs strikingly from all other *Steatocranus* except *uban-*

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Plate 11

a. *Nanochromis minor* new species, paratype, ♀, 21.0 mm. Zaire River near Kinganga (MCZ 50342).
b. *Nanochromis splendens* new species, holotype, ♂, 43.1 mm. Zaire River at Inga (MCZ 50476).
c. *Nanochromis splendens* new species, paratype, ♀, 35.4 mm. Zaire River at Inga (MCZ 50477).
d. *Steatocranus gibbiceps*, 84 mm. Zaire River at Inga (MCZ 50555).
e. *Steatocranus casuarius*, 67 mm. Zaire River at Inga (MCZ 50556).

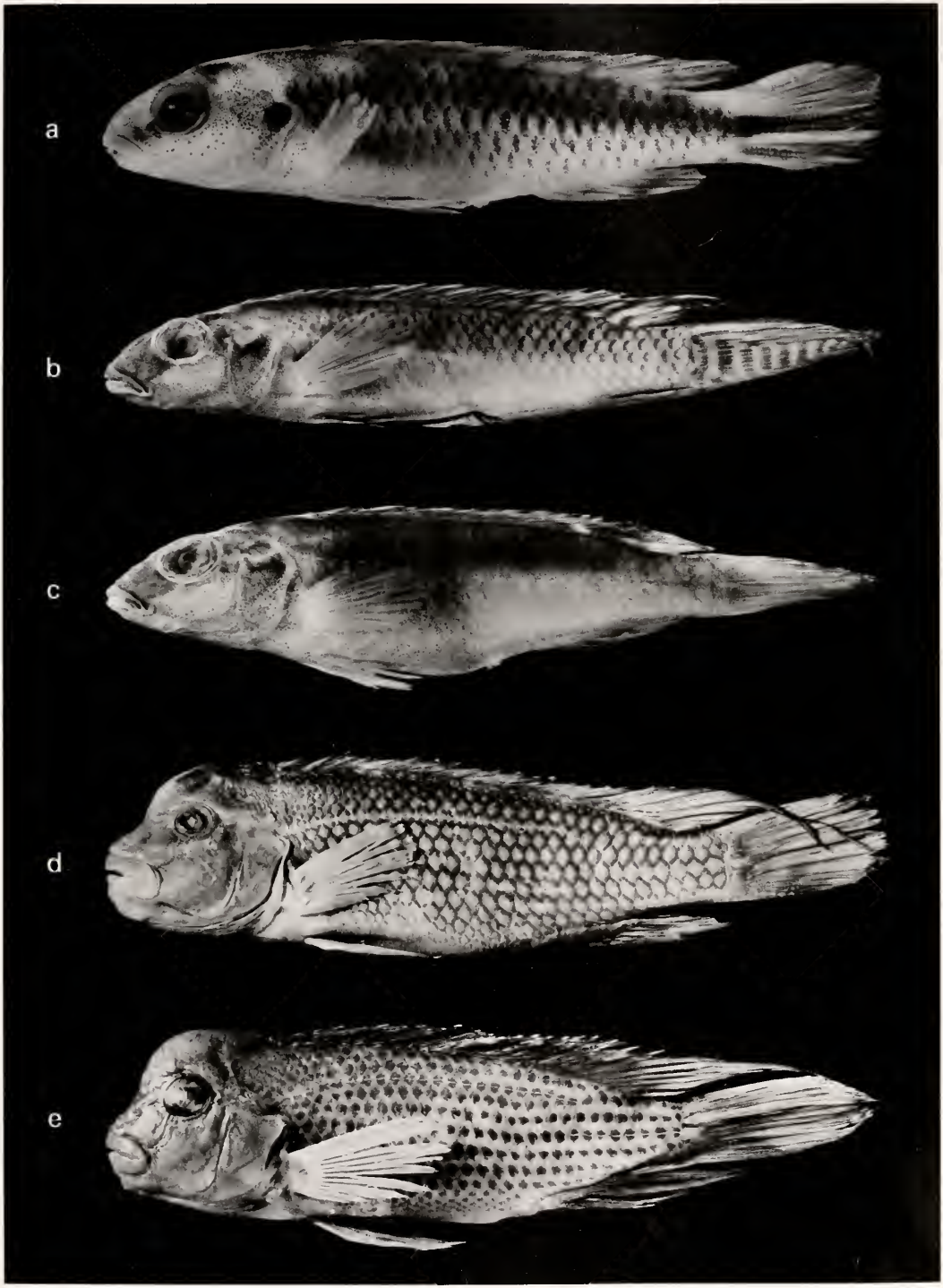

Plate 11

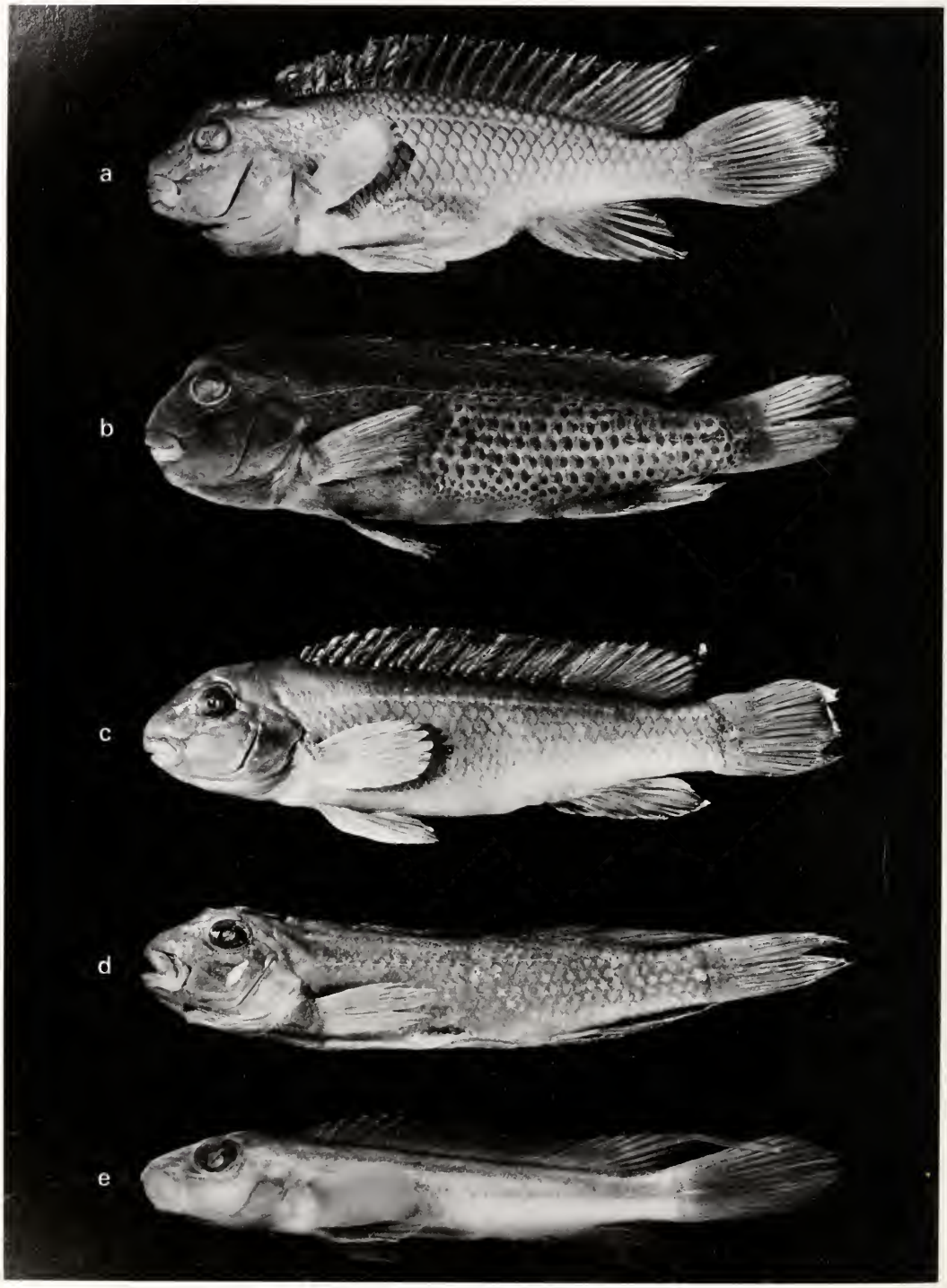

Plate 12

guiensis in coloration: scales with strongly contrasting dark center and light submargin. It differs from *ubanguiensis* in having a much shorter caudal peduncle, noticeably longer fins, longer head, larger eye, one or two more dorsal spines, and one more vertebra (Table 19).

Coloration. See diagnosis. Overall coloration dark brown in life, more than in *gibbiceps.* Branchiostegal membranes dusky cream-colored centrally, darkening towards the edges; breast dusky cream-colored.

Comments. *S. casuarius* and *gibbiceps* were found sympatrically in large numbers, including young, at most of our rapids localities (Table 3). They are immediately distinguishable at all sizes by the difference in coloration. Larger specimens of the two species differ strikingly in dentition and length of intestine. *S. casuarius* has an extremely long, highly coiled intestine (length about 1.5–3 times S. L.) and apparently feeds predominantly on algae. *S. gibbiceps* has a relatively short, uncoiled intestine (length about two-thirds to four-fifths S. L.) and feeds largely on gastropods, including *Septariellina congolensis,* which it swallows whole without crushing. This is the only *Steatocranus* in which we found snails in the stomach contents.

Steatocranus glaber new species
Plate 12, a

Holotype. MCZ 50557, 52.5 mm, R & S 41.
Paratypes. MCZ 50558, 18: 10.7–47.0 mm, R & S 41.

Diagnosis. Adult *glaber* are distinguished from all other *Steatocranus* by having large chisel-shaped teeth, with straight or only slightly notched cutting edges, in the outer tooth row of both jaws (Figure 7). The species differs strikingly from *casuarius* and *ubanguiensis* in coloration, and from *mpozoensis, rouxi, tinanti,* and *irvinei* in having only a single internal row of tricuspid teeth in each jaw. It is most similar to *mpozoensis* and *gibbiceps.* From *mpozoensis* it differs in having a terminal mouth, noticeably longer fins, and fewer gill rakers (Table 19). It differs from *gibbiceps* in dentition, in having the snout broadly rounded instead of narrow and relatively pointed, and in having a long, highly coiled intestine.

Coloration. Preserved specimens light brownish or greenish; scales with light centers and dark submargins as in *gibbiceps* but with less contrast; fins probably tinged with red in life; branchiostegal membranes and breast light brownish or dusky cream-colored.

Comment. In contrast to *casuarius,* the intestinal contents of *glaber* are noticeably opaque in radiographs, consisting largely of diatoms and sand grains cemented together.

Steatocranus ubanguiensis new species
Plate 12, b

Holotype. MCZ 50584, 52.8 mm, rivière Mbomou, a tributary of the Ubangui River, near Gozobangui, Central African Republic; T. R. Roberts, 29–30 May 1971.
Paratypes. MCZ 50585, 2: 45.3–46.3 mm, same locality as holotype.

Diagnosis. *S. ubanguiensis* is distinguished from all of its congeners in having an extremely steep forehead, shorter jaws and fewer teeth, and more reduced scales on the anterior half of the body and entire abdomen. It differs from all except *casuarius* by the coloration of its scales. It is

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Plate 12

a. *Steatocranus glaber* new species, holotype, 52.5 mm. Zaire River near Inga (MCZ 50557).
b. *Steatocranus ubanguiensis* new species, holotype, 52.8 mm. Rivière Mbomou near Gozobangui (MCZ 50584).
c. *Steatocranus mpozoensis* new species, holotype, 48.9 mm. Rivière Mpozo (MCZ 50582).
d. *Steatocranus rouxi,* 49 mm. Luluabourg, Kasai (AMNH 12358, holotype of *Steatocranus elongatus*).
e. *Steatocranus tinanti,* 36 mm. Zaire River near Gombe (MCZ 50160).

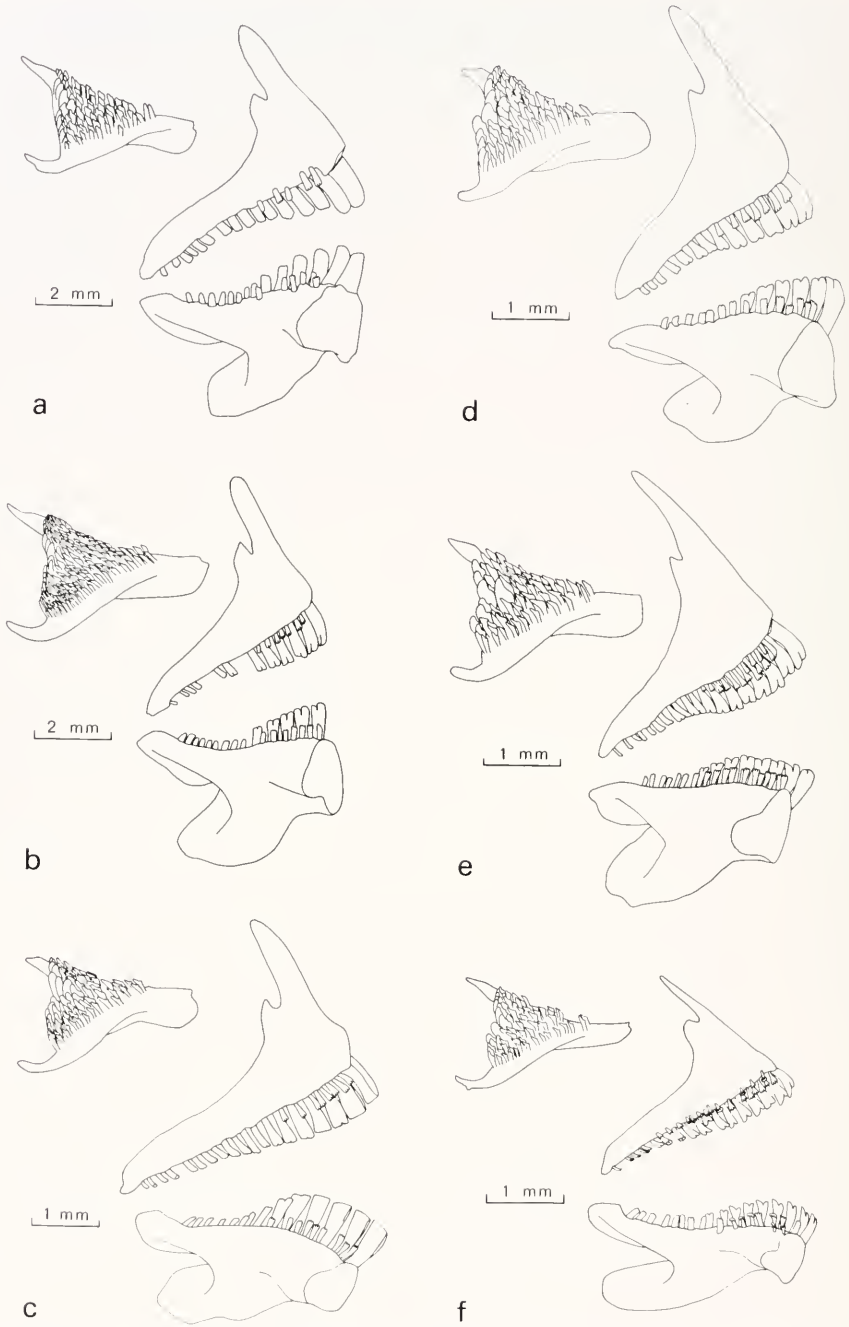

Figure 7. *Steatocranus*, dentition: a. *gibbiceps*, 74 mm; b. *casuarius*, 66 mm; c. *glaber*, 43 mm; d. *ubanguiensis*, 45 mm; e. *mpozoensis*, 50 mm; f. *tinanti*, 36 mm.

further distinguished from *casuarius* in having much shorter fins, a longer caudal peduncle, a shorter head, and a smaller eye (Table 19).

Coloration. Body dark brown, head dark brown or blackish; scales with a dark brown center and a light submargin, as in *casuarius*; branchiostegal membranes brownish centrally, with a sharply defined thin black margin.

Steatocranus mpozoensis new species
Plate 12, c

Holotype. MCZ 50582, 48.9 mm, R & S 74: rapids in rivière Mpozo a few km upstream from the bridge on the road from Kinshasa to Matadi. Lat. 5°51′S, Long. 13°31′E. Water 23.8°C, pH 8.5–9.0, O_2 8 ppm. 1 September 1973.

Paratypes. MCZ 50583, 25: 22.2–54.7 mm, same locality as holotype.

Diagnosis. A *Steatocranus* distinguished from all others in the Zaire basin in having an overhanging snout, the outer teeth in the upper jaw visible from below even when mouth is closed; fins relatively short. It differs from *casuarius* and *ubanguiensis* in coloration, and from *gibbiceps* and *glaber* in having the external row of jaw teeth all bifid and less massive (Figure 7). It differs from *irvinei* in having fewer gill rakers, a larger eye, and a narrower preorbital bone.

Coloration. Body greenish in life; fins tinged with red; center of scales light-colored and submargin darker but less pronouncedly so than in *gibbiceps* and *glaber*. Branchiostegal membranes yellowish green.

Comments. In *mpozoensis*, and also in *tinanti*, the upper lip is in some specimens joined to the skin of the snout by a median frenum and the upper jaws are relatively nonprotrusible. This is unusual in cichlids.

Steatocranus rouxi (Pellegrin) 1928
Plate 12, d

Leptotilapia rouxi Pellegrin, 1928: 112–113 (Luluabourg, Kasai); Pellegrin and Roux, 1928: 300–301, pl. 2, fig. 2 (illustration of holotype).

Steatocranus elongatus Nichols and LaMonte, 1934: 4–5, fig. 4 (Luluabourg).

Diagnosis. *S. rouxi* differs from all other *Steatocranus* in the Zaire basin in having 15–16 instead of 12 circumpeduncular scales; from *irvinei* it differs in having fewer gill rakers, fewer teeth, and a terminal rather than subterminal mouth. It further differs from *casuarius* and *ubanguiensis* in coloration and in morphometrics (Table 19), from *gibbiceps* and *glaber* in having the outer jaw teeth bifid and less massive, and from *gibbiceps, casuarius, glaber* and *ubanguiensis* in having two internal rows of tricuspid jaw teeth instead of only one.

Comments. This is perhaps the most generalized *Steatocranus*. Morphologically it appears to link the extremely elongate *tinanti* with the other members of the genus.

The type specimens of *S. elongatus* agree closely with the description and figure of *rouxi*, the types of which we have not examined. Our counts and measurements of the *elongatus* types are compared with Pellegrin's counts and measurements and some additional measurements made on the published figure of the holotype of *rouxi* in Table 20. It should be noted that the figure of the holotype of *elongatus* is erroneous with respect to dorsal profile and scale pattern; in these characters the holotype of *elongatus* closely resembles the figure of *rouxi*.

Pellegrin distinguished his genus *Leptotilapia* from *Steatocranus* on the basis of a more elongate body, two internal rows of tricuspid jaw teeth, and lack of a frontal gibbosity. Development of the gibbosity varies among individuals as well as among the species of *Steatocranus*; it is best developed in old males of *casuarius*. Nichols and LaMonte's specimens of *rouxi* have it better developed than Pellegrin's holotype. Although Nichols and LaMonte reported only a single inner row of jaw teeth in *elongatus*, we find that the type specimens actually have two.

TABLE 19. MORPHOMETRIC AND MERISTIC CHARACTERS IN *STEATOCRANUS*.

	gibbiceps[1]	*casuarius*[2]	*glaber*[3]	*ubanguiensis*[4]	*mpozoensis*[5]	*rouxi*[6]	*tinanti*[7]	*irvinei*[8]
n: S. L. mm	6: 51.0–83.5	6: 45.0–66.8	6: 31.0–52.5	3: 45.3–52.8	6: 46.4–54.7	2: 48.9–50.9	6: 38.5–62.6	6: 62.8–84.4
Head	29.2–32.4	32.2–33.9	30.1–31.9	29.0–29.2	28.0–30.3	28.8–30.3	28.9–32.4	31.2–34.5
Eye (% headlength)	21.0–26.1	26.5–31.0	24.5–29.2	24.2–26.7	21.9–26.4	24.0–25.5	23.6–28.3	17.1–21.6
Preorbital (% headlength)	16.8–22.1	17.9–19.0	15.6–20.3	20.5–21.6	15.7–18.6	17.7–19.5	13.6–19.4	25.9–31.9
Depth	25.1–28.7	30.0–32.3	27.7–30.1	29.0–29.8	24.4–26.5	22.3–24.8	15.5–23.4	26.0–28.4
Last dorsal spine	10.4–14.8	14.9–17.8	14.5–17.5	12.1–14.3	10.2–12.7	12.0–12.1	10.0–12.7	12.6–13.5
Longest dorsal ray ♂	29.9–39.9	33.9–44.2	36.1–47.2	16.1–17.7	19.8–32.9	31.5–34.2	22.1–34.5	17.5–27.3
Last anal spine	10.4–12.7	15.7–18.0	12.8–14.3	10.4–11.9	8.7–11.3	11.4–11.7	7.5–11.7	8.1–12.6
Longest anal ray ♂	22.3–36.0	30.8–34.1	24.2–33.5	16.8–18.4	20.2	20.0–24.4	19.6–30.0	15.9–22.4
Pectoral fin	21.4–24.6	24.4–27.2	22.1–24.0	22.5–23.1	19.2–21.3	19.4–21.5	19.4–22.8	19.7–25.1
Pelvic fin	24.1–27.2	28.1–29.2	23.8–27.1	21.4–24.3	21.6–23.4	22.7–24.6	21.0–27.3	18.2–23.8
Caudal fin	25.3–30.6	32.2–36.5	27.7–29.8	23.1–23.9	22.2–24.5	25.2–25.5	25.5–28.0	17.5–26.1
Length caudal peduncle/ height caud. ped.	1.21–1.35	0.89–1.07	1.28–1.48	1.21–1.41	1.20–1.39	1.25–1.50	1.49–1.89	1.27–1.41
Dorsal spines	19–20	20–21	19–21	19	20–21	20	21–22	20–21
Dorsal rays	7–8	6–7	6–7	7	8	7	7–8	8
Lateral line scales	30–32	30–31	30–32	30–31	31–32	31–32	33–34	32–34
Upper pored scales	20–21	21–23	20–21	22–23	21–24	20–22	21–22	24–26
Lower pored scales	8–10	8–9	9–11	7–8	8–10	8–9	9–12	7–9
Circumped. scales	12	12	12	12	15–16	12	12	16
Outer teeth, upper jaw	27–37	32–38	32–41	26–30	32–36	34–36	35–54	48–56
Gill rakers	6–7	6–7	6–7	6	8	5–6	6–8	11–12
Anterior + posterior vertebrae	14–15+14–5	15–16+13–14	15–16+14–15	14+14	14–16+14–15	14–15+15–16	15–16+15–16	16–17+14–15
Total vertebrae	28 (1); 29 (6); 30 (1)	29 (8)	29 (4); 30 (2)	28 (3)	29 (1); 30 (7)	29 (1); 31 (1)	31 (5); 32 (3)	31 (6)

[1] MCZ 50555 (R & S 41). [2] MCZ 50480 (R & S 38). [3] MCZ 50557–7 (holotype and paratypes). [4] MCZ 50585–6 (holotype and paratypes). [5] MCZ 50583–4 (holotype and paratypes). [6] AMNH 12358 and 12449 (holotype and paratype of *Steatocranus elongatus*). [7] MCZ 48003 (Kinsuka). [8] UMMZ 195059 (Volta River at Akosombo).

Table 20. Comparison of the nominal species *Steatocranus elongatus* Nichols and LaMonte 1934 with its senior synonym *Steatocranus rouxi* (Pellegrin) 1928.

	rouxi[1]	*elongatus*	
	Holotype	Holotype	Paratype
S. L. mm	60	48.9	50.9
Head	27.8	28.8	30.3
Orbit (% headlength)	28.7	25.5	24.0
Interorbital (% headlength)	14.4	15.6	13.6
Snout (% headlength)	43.1	39.7	41.5
Depth	21.3	22.3	24.8
First dorsal spine	4.0*	2.2	1.4
Third dorsal spine	5.7*	5.9	6.1
Last dorsal spine	12.3	12.1	12.0
Longest dorsal ray	41.3	31.5	34.2
Third anal spine	10.3*	11.7	11.4
Longest anal ray	23.9*	20.0	24.4
Pectoral fin	20.8	21.5	19.4
Pelvic fin	24.6*	22.7	24.6
Length caudal peduncle	14.0*	16.0	14.7
Depth caudal peduncle	10.9*	10.6	11.8
Caudal fin	25.0	25.2	25.5
Dorsal fin	XX,8	XX,8	XX,8
Anal fin	III,7	III,7	III,7
Pectoral fin	i,12	ii,13	ii,12
Upper pored scales	22	20	22
Lower pored scales	9	9	8
Midlateral scales	34	32	31
Circumpeduncular scales	16	16	15
Tooth rows	3	3	3
Outer teeth, upper jaw	42	34	36
Gill rakers	5	6	5

[1] Measurements calculated from Pellegrin's original description, or, for those marked*, taken from the figure of the holotype published by Pellegrin and Roux, 1928: plate 2, figure 2.

Steatocranus tinanti (Poll) 1939
Plate 12, e

Gobiochromis tinanti Poll, 1939:48–49, fig. 31 (Léopoldville).
Leptotilapia tinanti Poll, 1957:139.

Diagnosis. A very distinctive *Steatocranus*, differing from all others in its very elongate body, distinctive coloration, longer caudal fin, more numerous lateral line scales, and superolateral eyes.

Coloration. A pair of longitudinal bands, light dusky brown, extend the length of the body, converging posteriorly; the upper band runs between the base of the dorsal fin and the upper row of pore-bearing scales, the lower band being midlateral in position. Rest of body dusky cream-colored, head dark dusky brown, lightening on cheeks. Branchiostegal membranes cream-colored or dusky brown.

Steatocranus irvinei (Trewavas) 1943

Gobiochromis irvinei Trewavas, 1943:186, figs. 1–2 (Volta River at Senchi Ferry).
Leptotilapia irvinei Trewavas and Irvine, 1947: 277, fig. 183 (abstract of original description; color note on live or freshly preserved specimens).

Diagnosis. A *Steatocranus* distinguished from all others in having scales on the opercle; a relatively small, high-set eye, with a wide preorbital bone; and 11–12 gill rakers on the first gill arch, including two or three on its upper limb. The jaw teeth are smaller and more numerous than in any other species, and are arranged in four rows in both jaws rather than only two or three rows. Teeth in internal rows of lower jaw predominantly conical, rather than predominantly tricuspid. Adults commonly grow to 150 mm; the largest Zaire *Steatocranus* are about 90 mm.

In having an overhanging snout and subterminal mouth, *irvinei* agrees with *mpozoensis* but differs from all other Zaire *Steatocranus*.

A detailed description of *irvinei* is given by Trewavas (1943). We have examined six freshly preserved specimens (UMMZ 195059) collected from the Volta River in the tailwaters of the dam at Akosombo by D. J. Stewart in June, 1973. Trewavas and Irvine (1947) recorded the color as dark greyish green; our specimens are dark bluish black, especially on the head, branchiostegal membranes, and dorsal, anal, and pelvic fins, and dark brown or blackish brown on the breast and belly.

Comment. If the *Steatocranus* species from the Zaire basin and *irvinei* from the Volta basin represent a monophyletic group, the geographical distribution of this genus offers an interesting parallel to that of the rheophilic mormyrid *Campylomormyrus tamandua*.

TABLE 21. MORPHOMETRIC AND MERISTIC CHARACTERS IN *TELEOGRAMMA*.

	gracile	*brichardi*	*depressum*[1]	*monogramma*[2]
Largest ♂ S. L. mm	70.6	79.9	95.1	60.8
Largest ♀ S. L. mm	54.8	63.6	70.9	67.6
Interorbital	5.2–5.9	4.6–6.2	6.3–7.5	3.8–4.4
Depth of body	14.9–16.1	15.8–17.4	10.5–12.3	14.2–15.8
Width of body (% bodydepth)	104–115	84–106	136–166	87–106
Sixth dorsal spine	7.1–8.7	8.5–12.6	4.9–7.4	10.4–12.6
Total dorsal elements	29(1) 30(7) 31(2)	29(4) 30(6)	31(10)	29(3) 30(3) 31(1)
Dorsal spines	22(1) 23(5) 24(4)	22(2) 23(8) 24(1)	23(1) 24(9)	20(7)
Dorsal rays	6(2) 7(8)	6(4) 7(5) 8(1)	7(9) 8(1)	9(3) 10(3) 11(1)
Total anal elements	12(4) 13(4) 14(2)	13(5) 14(4) 15(1)	14(4) 15(6)	12(1) 13(4) 14(2)
Anal spines	5(8) 6(2)	4(1) 5(9)	5(7) 6(3)	4(7)
Anal rays	7(6) 8(2) 9(2)	8(4) 9(5) 10(1)	8(1) 9(5) 10(4)	8(1) 9(4) 10(2)
Pored scales	33–35	49–56	46–58	33–35
Scales above lat. line ±	87–95	70–80	90–110	51–59
Circumpeduncular scales	23–25	24–27	23–26	17–19
Gill rakers (2nd arch)	8(3) 9(7)	11(4) 12(8) 13(2)	10(4) 11(2) 12(3)	8(2) 9(4) 10(1)
Precaudal vertebrae	13(2) 14(11) 15(3)	13(10) 14(4)	13(2) 14(20)	13(3) 14(4)
Caudal vertebrae	17(2) 18(11) 19(3)	18(4) 19(10)	18(9) 19(3)	18(1) 19(3) 20(3)
Total vertebrae	31(1) 32(12) 33(3)	31(1) 32(15)	32(10) 33(11)	32(1) 33(6)

[1] Types. [2] AMNH 12384, Luluabourg, Kasai.

Teleogramma Boulenger 1899

Type species: *Teleogramma gracile* Boulenger 1899, by original designation.

An endemic Zairean genus of exceptionally elongate, highly rheophilic cichlids, with small cycloid scales and a single continuous row of lateral line scales. Longest soft ray in pelvic fin is the third or middle ray. Jaws with bands of fine unicuspid teeth and a few enlarged anterior canines, as in *Lamprologus*. Pharyngeal teeth unicuspid or weakly bicuspid, nonmolarized. Dorsal fin with 20–24 spines, anal with four to six. The only other African cichlid with a single continuous row of lateral line scales is *Gobiocichla*, a less elongate form with multicuspid jaw-teeth and only 13 dorsal spines endemic to the Niger River.

Teleogramma comprises four species, one known only from Kasai, the other three from the rapids of the Lower Zaire River. Females, usually smaller than males, are characterized by having the thin red margin on the lappets of the spinous dorsal fin and on the soft dorsal continued as a broad swath on the upper lobe of the caudal fin. In males the caudal fin is either uniformly dark in color, or has only a very thin red margin on the upper lobe. This particular dichromatism is not found in any other cichlids. Counts and measurements for all of the species are presented in Table 21.

Teleogramma gracile Boulenger 1899 Plate 13, a–b

Diagnosis. A *Teleogramma* distinguished from each of the other species by slight but consistent differences in morphometrics, and from all of them by having fewer anal-fin rays (7–9, with a mode of 7, versus 8–10, with a mode of 9). It is the only

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Plate 13

a–b. *Teleogramma gracile*, ♂, 59 mm, and ♀, 46 mm. Zaire River at Bulu (MCZ 50252).
c. *Teleogramma monogramma*, ♂, 63 mm. Luluabourg, Kasai (AMNH 12384).
d–e. *Teleogramma brichardi*, ♂, 73 mm. Zaire River at Kinsuka (MCZ 48008).
f–g. *Teleogramma depressum* new species, holotype, ♂, 90.0 mm. Zaire River at Inga (MCZ 50482).

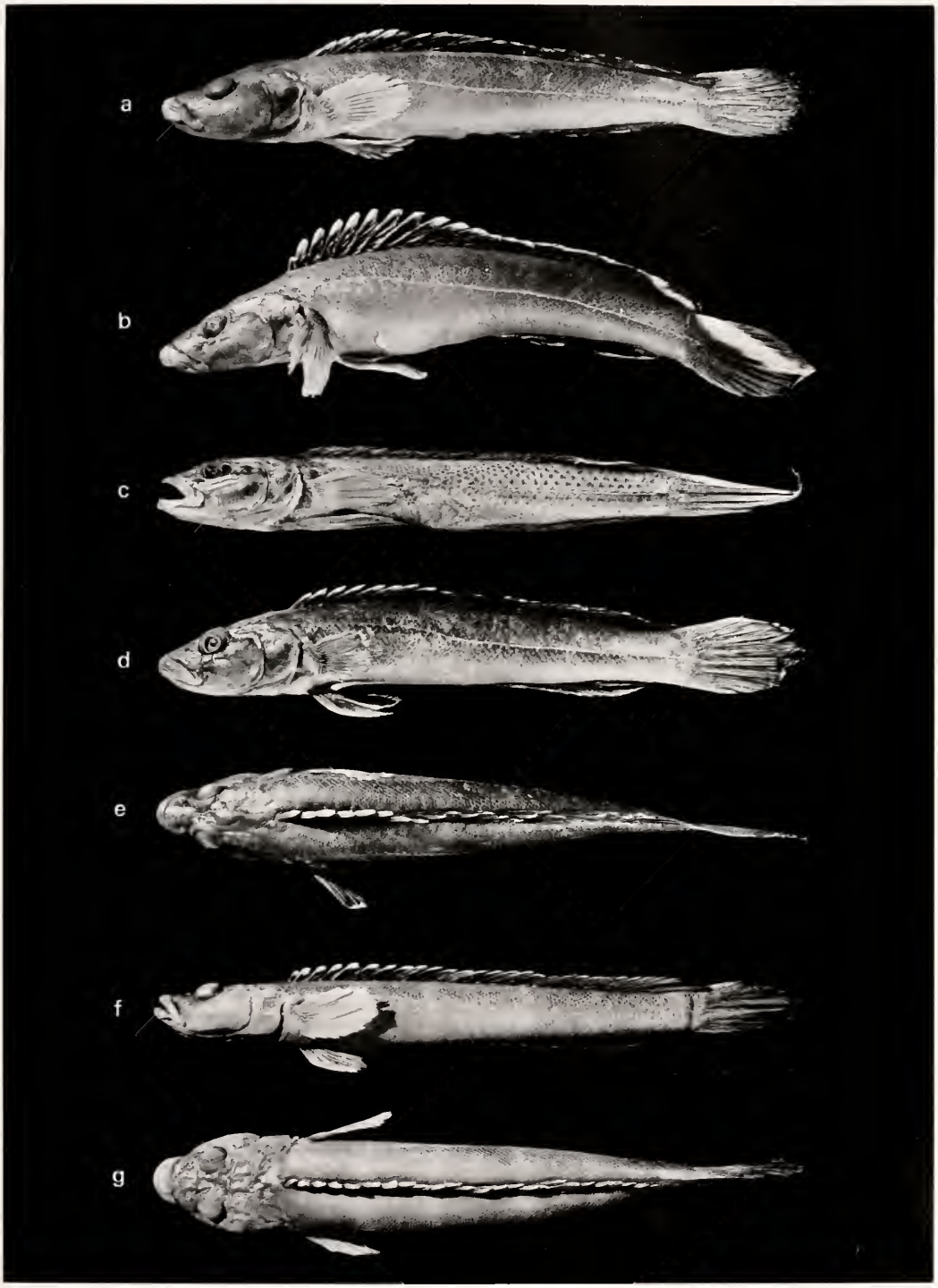

Plate 13

species in which females have a broad black margin above the red area on the upper lobe of the caudal fin (Plate 13, b). It further differs from *brichardi* and *depressum,* its congeners in the rapids of the Lower Zaire River, in having only 33–35 pored lateral line scales (versus 46 or more), and only 8–9 gill rakers on the second gill arch (versus 10 or more). From *monogramma* it differs in having 22–24 dorsal spines instead of only 20, and much smaller scales above and below the lateral line scale row.

Teleogramma monogramma (Nichols and LaMonte) 1934
Plate 13, c

Diagnosis. T. monogramma differs from its congeners in having a dorsal fin with 20 spines and 9–11 rays; relatively large scales above and below the series of pored lateral line scales; and a narrower interorbital space (3.8–4.4, versus 4.6 or more). (Coloration of caudal fin in females unknown).

Teleogramma brichardi Poll 1959
Plate 13, d–e

Diagnosis. A relatively compressed *Teleogramma,* body depth 15.8–17.4; pored lateral line scales 49–56, scales impinging directly on lateral line series from above about 70–80. Females with uppermost portion of caudal fin entirely red.

Comment. This species, fairly abundant in the rapids near Kinsuka, has not been found elsewhere.

Teleogramma depressum new species
Plate 13, f–g

Holotype. MCZ 50482, 90.0 mm, R & S 38.

Paratypes. MCZ 50161, 18:32.1–59.9 mm, R & S 2; MCZ 50396, 17:24.4–76.2 mm, R & S 28; MCZ 50483, 63:17.0–84.8 mm, R & S 38; MCZ 50559, 19:28.8–95.1 mm, R & S 41.

Diagnosis. A very distinctive *Teleogramma,* with a more flattened head and body than any other known cichlid; width of body from one and a third to one and two-thirds greater than depth of body; interorbital space broad, 6.3–7.5 (compare dorsal views of *brichardi* and *depressum* in Plate 13); dorsal fin spines and rays distinctly shorter than in other *Teleogramma*; pored lateral line scales 46–58, with about 90–110 scales impinging on them from above (Table 21). Females with a thin black margin above the red on the upper lobe of caudal fin.

Mastacembelus Scopoli 1777

Type species: *Mastacembelus mastacembelus* (Solander, *in* Russell) 1794 (see Wheeler, 1956).

Mastacembelus are eel-like fishes, without pelvic fins, and with 7–40 detached, depressible spines in the anterior portion of the dorsal fin. There are 15 species in Asia and at least 50 in Africa. Our rapids collections include eight species; three are new, and differ from all previously known *Mastacembelus* in lacking scales.

Our vertebral counts in *Mastacembelus* and their definitions are as follows: total vertebrae = all vertebrae with a complete and separate centrum counting that in urophore as one; predorsal vertebrae = vertebrae anterior to first dorsal pterygiophore; abdominal vertebrae = vertebrae anterior to first anal pterygiophore; and caudal vertebrae = vertebrae posterior to last abdominal vertebra and having a complete and separate centrum.

Mastacembelus marchei Sauvage 1879

Mastacembelus marchei Sauvage, 1879:1 (la chute de Doumé, dans le pays de Adouma, haut Ogôoué); Sauvage, 1880:36–37, pl. 1, fig. 1 (illustration of holotype).

Diagnosis (after Sauvage). A *Mastacembelus* with two preopercular spines; length of head seven times into length of body; dorsal fin with 24 spines and 78 rays, anal with two spines [probably an error] and 80 rays.

The illustration of the holotype apparently shows the color pattern well. The following description of the coloration is translated from Sauvage (1880):

body brownish, widely marbled with yellow; a series of black spots, large and regular, on the back and at the base of the anal fin; side of the head black; underside of body with a uniformly yellowish tint; anal fin with a black border; tip of caudal fin white, with a wide, black band; posterior portion of soft dorsal fin bearing some black spots, anterior portion small, irregular deep-colored spots, uniting to form three bands; pectoral fins colorless.

Dr. Thys van den Audenaerde kindly supplied the following information about the type locality: "the falls at Doumé are on the Ogowé River some 30–50 km upstream and to the east of Lastoursville, in a forested area about 250–260 m above sea level, between 0°50 and 1°01′S and 12°56 and 13°11′E."

The specimens we questioningly refer to *marchei* agree with Sauvage's brief description in most respects, except in having slightly more dorsal fin spines, three anal spines instead of two, and in coloration. The difference in coloration, however, is so great and so consistent that we suspect our specimens represent an as yet undescribed species, probably endemic to the Zaire basin.

Our specimens have a strong preorbital spine and two strong preopercular spines. Radiographs of several reveal the dorsal fin has 25–27 spines (the last spine hidden) and about 75–92 rays; anal fin with three spines (last hidden) and about 77–78 rays; predorsal vertebrae 5–6; abdominal vertebrae 29–30; caudal vertebrae 47–50; total vertebrae 77–79. The largest specimens tend to have the head and body uniformly light grey or brownish grey on the back and sides, becoming lighter still on the lips, cheek, and undersides of head and abdomen. Median fins dark brownish grey basally, with a light margin. Pectoral fins uniformly light. In the smaller specimens from R & S 41 the general coloration is similar to that described for larger specimens, except that several have a series of light-colored, roundish spots on the dorsal midline and dorsal fin. A large series of half-grown specimens from the rivière Mbomou in Ubangui (MCZ 50590) have similar coloration, except that the entire head and body are of a darker, browner hue, and the light-colored spots on the back and dorsal fin stand out more sharply.

Comment. Two specimens from Malebo Pool, identified as *marchei* by Poll (1959: 111–112) apparently represent the same species as our material.

Mastacembelus paucispinis Boulenger 1899

Mastacembelus paucispinis Boulenger, 1899:55, pl. 28, fig. 3 (Matadi).

Diagnosis. A *Mastacembelus* distinguished from all others by having only 7–10 dorsal spines (the species with the next lowest number of dorsal spines having 19 or more); dorsal rays in excess of 100, up to 125; origin of soft dorsal fin midway between occiput and a vertical line through origin of anal fin; anal fin with three spines and 79–83 rays; a preorbital spine and two preopercular spines; total vertebral count 81–83; predorsal vertebrae 4 or 5 (usually 5); abdominal vertebrae 28–29; caudal vertebrae 51–55.

Coloration. Largest specimens dark violaceous blue on back and sides, underside of head and abdomen lightened; median fins of same color as back and sides, except for white distal margin of anal and caudal; back and dorsal fin in some specimens with small, indistinct whitish marks or mottling; pectoral fin dark, with white spots or mottling. In smaller specimens the body and fins are much more distinctly mottled; specimens over about 150 mm S. L. have a distinctly violaceous blue tint on the back and sides, but specimens smaller than that tend to be brownish on the back and sides, and much lighter on the ventral surfaces. The coloration of juveniles as well as adults is unlike that in any other *Mastacembelus* in the rapids. The coloration of *M. congicus* is more ornate or detailed, on the fins as well as on the body; adults do not assume a dark violaceous blue

tinge and their ventral surface is much whiter than in *paucispinis*.

Comments. The holotype of this species was obtained at Matadi, without indication of habitat; Poll (1959:145) reported a specimen from the rapids at Kinsuka. We found it in the midst of extensive rapids, in areas where the bottom is predominantly coarse sand. Other *Mastacembelus* in these areas were *M. congicus* and *M. brachyrhinus*.

Mastacembelus brachyrhinus Boulenger 1899
Plate 14, a

Mastacembelus brachyrhinus Boulenger, 1899:55–56, pl. 28, fig. 4 (Matadi).

Diagnosis. A microphthalmic *Mastacembelus* with no preorbital spine; a strong preopercular spine; eye normally developed; dorsal fin with 30–32 spines and 63–70 rays; anal fin with three spines and 62–67 rays; total vertebral count 77–80; predorsal vertebrae 5; abdominal vertebrae 32–34; caudal vertebrae 44–46; principal caudal rays 5 + 5. (All of these counts, except "principal caudal rays," are based on at least 10 specimens; the dorsal spine counts are based on all 39 of our specimens and the count of the holotype given by Poll, 1959.)

Coloration. Adults variable, either uniformly dark brown, brownish black or black, or else brownish or greyish brown with numerous light-colored, round or oval blotches. Most of the small specimens from R & S 29 are brownish with light-colored round spots relatively larger and better defined than in adults. There is no indication that living specimens undergo rapid color change.

Comments. This species, otherwise known only from the holotype, collected at Matadi without indication of habitat, was found at three of our rapids localities. It is of special interest because of its close relationship, possibly ancestral, to *Mastacembelus brichardi*.

Mastacembelus brichardi (Poll) 1958
Plate 14, b

Caecomastacembelus brichardi Poll, 1958:388; Poll. 1959:112–115 pls. 20 and 26.

Diagnosis. A strongly cryptophthalmic *Mastacembelus*, with eyes deeply embedded in the head, not visible at the surface; body more or less depigmented; no preorbital spine; a single, strong preopercular spine; dorsal fin with 27–30 (usually 28 or 29) spines and 55–60 rays; anal fin with three spines and 59–63 rays; body bilaterally compressed, much deeper than wide, covered with small scales; total vertebral count 71–73; predorsal vertebrae 4; abdominal vertebrae 28–29; caudal vertebrae 42–44; principal caudal rays 5 + 5. (All of these counts, except "principal caudal rays," are based on 30 or more specimens.)

Coloration. Coloration variable. Some specimens entirely milky white or pinkish in life, with no melanophores on the head or body. At the other extreme are specimens with fine melanophores rather uniformly distributed over the back and sides, producing a decidedly dusky appearance. Some specimens have a faint mottling on the dorsal portions of head and body. Juveniles exhibit the same range of coloration as adults, and all populations exhibit considerable variation. They do not seem to be capable of rapid changes of coloration. Poll (1959, pl. 26, fig. 2) published a photograph of a specimen in which the pigmentation is much darker and mottling more pronounced than in any specimens collected by us, possibly produced by keeping the specimen in a well-lit aquarium before it was preserved.

Comment. Although Poll recognized the close relationship between this species and *M. brachyrhinus*, he proposed a new genus for it because of its depigmentation and "lack" of eyes. In doing so, he cited as precedent the case of *Caecorhamdia* Norman 1926, erected for a blind "species" otherwise virtually identical to the widely distributed and highly variable *Rhamdia quelen*. Loss of the eyes, and the depigmentation usually

associated with it, is a loss or reduction character likely to occur independently without other notable change, especially in genera such as *Rhamdia* and *Mastacembelus* in which the eyes are normally small and of secondary importance. The objection to recognizing a genus based on a single character of this nature is that there is no way to determine whether the several species that may eventually be referred to the genus evolved independently. It is contrary to the objectives of phyletic classification to follow a procedure that will inevitably result in polyphyletic taxa. For this reason we have not designated a new genus for *Lamprologus lethops,* and would not recognize *Caecobarbus, Typhlobagrus, Anoptichthys,* or other "genera" distinguished solely on the absence of eyes and superficial pigmentation.

Mastacembelus brichardi is the most abundant member of the genus in our collections from the rapids. Large numbers of them were present at five of the nine principal collecting stations. We found it together with *M. brachyrhinus* only at R & S 29, along with a small number of specimens morphologically intermediate between them, which we tentatively interpret as interspecific hybrids.

Mastacembelus brachyrhinus × *M. brichardi*
Plate 14, c

MCZ 50256, 6:26–145 mm, R & S 29.

The eye in these specimens, while lying at the surface and appearing normally developed, is not so large as in *brachyrhinus,* its diameter 0.5–1.0% S. L. in specimens 91–145 mm. Their coloration is uniform dark brownish, without lighter marks even in the smallest specimen, as dark as some less pigmented *brachyrhinus,* and much darker than *brichardi.* They are intermediate between *brachyrhinus* and *brichardi* in all meristic characters. The following counts were obtained from radiographs: dorsal spines 29(4), 30(1); anal rays 58–66; total vertebrae 74(1), 75(2), 76(2); predorsal vertebrae 4(3); abdominal vertebrae 30(1), 31(2), 32(2); and caudal vertebrae 44(5).

Samples of *brichardi* obtained at our other localities did not include any specimens with eyes superficial in position or with comparably intermediate meristic characters. The large sample from R & S 38, however, does include a specimen in which the eye is much closer to the surface than in typical *brichardi.* This 98-mm individual has 30 dorsal spines and is exceptionally darkly pigmented, but in all other respects it agrees with *brichardi.* That a population of *brichardi* can produce individuals with some *brachyrhinus*-like characters suggests that they may be one and the same species.

Mastacembelus crassus new species
Plate 14, d

Holotype. MCZ 50257, 134.0 mm, R & S 29.
Paratypes. MCZ 50258, 176:34.6–157.8 mm, R & S 29; MCZ 50318, 14:54.0–122.5 mm, R & S 35; MCZ 50400, 1:75.5 mm, R & S 28.

Diagnosis. A *Mastacembelus* in which juveniles as well as adults have a very thick head and body, the body nearly round in cross section and entirely scaleless; no preorbital or preopercular spines; weakly cryptophthalmic; eye minute, .6–1.1, decreasing in relative size with growth; dorsal fin with 20–21 (usually 20) spines and 52–61 rays; anal fin with two spines and 51–61 rays; total vertebral count 63–67; predorsal vertebrae 4 or 5 (usually 5); abdominal vertebrae 22–24; caudal vertebrae 41–44; principal caudal rays 4+4 or 4+3.

Coloration. Coloration highly variable. A very few specimens are entirely depigmented, milk-white, or pinkish in life, cream-colored after preservation. Most individuals are counter-shaded, with depigmented abdomens, and grey marblings or variegations dorsally. In some specimens marbling extends onto the belly. A few are almost uniformly grey except for a clearly defined depigmented area on the belly, mottled lips, and mottled median

Plate 14

fins. In none is the body uniformly grey. The distal portions of the median fins are usually depigmented, although sometimes they are mottled. Coloration of adults and juveniles is similar. They do not appear capable of rapid color change.

The eyes are approximately the same relative size in all specimens, regardless of the degree of pigmentation. In five of the most darkly pigmented specimens, 80–130 mm, eye diameter is .6–.7, and in five exceptionally light-pigmented individuals 94–144 mm, .6–.8.

Comments. This species was found only in the most extreme rapids habitats, in areas with predominantly rock-rubble bottom, and always with large numbers of *M. brichardi*. Radiographs of 20 *crassus* and 20 *brichardi* revealed snails in the stomachs of several *brichardi* but not in *crassus*. The snails are *Bulimus* (*Parabithynia*). We find no evidence of morphological intergradation between the two species.

Mastacembelus latens new species
Plate 14, e

Holotype. MCZ 50529, 65.0 mm, R & S 29.
Paratypes. MCZ 50530, 2:47.6–72.0 mm, R & S 29.

Diagnosis. A weakly cryptophthalmic and incompletely depigmented *Mastacembelus*; body bilaterally compressed, completely scaleless, and more elongate than in *brichardi*; no preorbital or preopercular spines. Dorsal fin with 21–24 spines and 55–58 rays; anal with 2 or 3 spines and about 58–62 rays. Total vertebrae 67–69; predorsal vertebrae 4; abdominal vertebrae 28–29; caudal vertebrae 67–69. Principal caudal rays 3 + 3.

Coloration. The smallest of our three specimens, 47.6 mm, is almost completely depigmented, the only melanophores being a few small, scattered clusters of tiny melanophores mostly on the posterior half of the body. In the two larger specimens, melanophores are more numerous and relatively conspicuous, concentrated on the dorsal surface of the head, along the dorsal midline of the body, and on the dorsal fin (Plate 14, e). Background coloration in all three specimens white or yellowish cream-color.

Comment. Numerous *brichardi* and *crassus* of comparable length were taken simultaneously with the type specimens of *latens*; all individuals were readily assigned to species at the first glance.

Mastacembelus aviceps new species
Plate 14, f

Holotype. MCZ 50564, 124.5 mm, R & S 41.
Paratypes. MCZ 50565, 9:49.7–106.5 mm, R & S 41; MCZ 50487, 17:39.9–112.1 mm, R & S 38.

Diagnosis. A *Mastacembelus* with the body elongate and round in cross section, depth of body 5.9–6.9, and width of body 5.0–7.5; head flattened; no preorbital or preopercular spines; scales absent; dorsal fin with 20–22 spines and 44–52 rays; anal fin with two spines and 49–52 rays; total vertebral count 61–65; predorsal vertebrae 3–5; abdominal vertebrae 22–24; caudal vertebrae 38–42; principal caudal rays 3 + 3.

Coloration. Coloration similar in all specimens: uniformly olivaceous or drab dorsally, grading to dull cream on abdomen and flanks.

Comments. Although *aviceps* agrees with *crassus* in lacking spines on the head, in

←

Plate 14

a. *Mastacembelus brachyrhinus*, 143 mm. Zaire River at Bulu (MCZ 50254).
b. *Mastacembelus brichardi*, 124 mm. Zaire River at Bulu (MCZ 50255).
c. *Mastacembelus brachyrhinus* × *Mastacembelus brichardi*, 145 mm. Zaire River at Bulu (MCZ 50256).
d. *Mastacembelus crassus* new species, holotype, 134.0 mm. Zaire River at Bulu (MCZ 50257).
e. *Mastacembelus latens* new species, holotype, 65.0 mm. Zaire River at Bulu (MCZ 50259).
f. *Mastacembelus aviceps* new species, holotype, 124.5 mm. Zaire River at Inga (MCZ 50564).

lacking scales, and in having similar meristic characters (except the lower anal ray count in *aviceps*), they are very different in other respects, and in fact, *aviceps* does not closely resemble any other known species. One of the localities where we found *aviceps* was in an extensive area of rocks and muddy bottom, the mud of about the same color as the body of *aviceps*. This is in marked contrast to the bottoms of rock rubble or rocks and coarse sand where we encountered other *Mastacembelus*. Nevertheless, *aviceps* lives in a rapids habitat as extreme as that of any of the others.

REPRODUCTION

Little is known about reproduction in the fishes of the Lower Zaire rapids. External fertilization apparently is the unbroken rule; we did not find nor do we know of any definite evidence for internal development or even internal fertilization in any of the species encountered in the rapids. Mature males of amphiliid and mochokid catfishes often have elongated genital papillae which terminate in a pore, and could conceivably function as intromittent organs (even more elongate genital papillae of similar appearance occur in mature males of the Andean catfish family Astroblepidae). None of the rapids fishes have been found with internally developing embryos, so that if internal fertilization does occur, it is presumably followed by egg-laying, rather than viviparity. Among the rapids Cichlidae, the only ones known to brood the eggs in their mouth are *Haplochromis*. So far as known, the others are substrate spawners, attaching the eggs to rocks.

As can be seen from Table 3, no fewer than 54 of the 129 species taken by our rapids survey are represented by young of 30.5 mm or less in standard length. The following 28 species are represented by young of 20.5 mm or less, which means they must have been spawned within a matter of days or at most a few weeks only before we collected them:

Microthrissa minuta
Myomyrus macrodon
Myomyrus pharao
Stomatorhinus sp. or spp.
Alestes macrolepidotus
Distichodus antonii
Distichodus sexfasciatus
Distichodus fasciolatus
Barilius lujae
Garra congoensis
Labeo nasus
Labeo sorex
Labeo sp. or spp. other than *sorex* and *nasus*
Chrysichthys cf. *cranchii*
Notoglanidium pallidum
Haplochromis demeusii
Haplochromis polli
Lamprologus cf. *moquardii*
Lamprologus werneri
Nanochromis parilus
Nanochromis splendens
Steatocranus gibbiceps
Steatocranus casuarius
Steatocranus tinanti
Steatocranus glaber
Teleogramma gracile
Teleogramma depressum
Mastacembelus brichardi.

Young as small as 20 or 30 mm have seldom been reported for fishes inhabiting any of the larger African rivers. Most of the species for which we collected young of 30.5 mm or less are otherwise known only from half-grown or adult specimens. This is particularly true for the taxa Mormyridae, Bagridae, Mochokidae, *Distichodus,* and *Labeo.* In most large African rivers, especially those of the so-called "sand-bank" category, it is very difficult to collect the young of many species, because their strongly seasonal reproductive activities are restricted to periods of steadily rising water. By the time the flooding has receded, the rapidly growing young are no longer this small. Due to its relative stability, the mainstream of the Lower Zaire River apparently offers a major exception to this general rule. One would expect, *a priori,* that here reproduction would be less

seasonal than in other African rivers, and our data support this hypothesis.

ADAPTATIONS

The 129 fish species in our collections from the Lower Zaire rapids can be grouped into four broad categories based on the degree or nature of their specialization to the rapids environment: 1) poorly adapted; 2) moderately adapted; 3) highly adapted to habitats exposed to strong current (rheophilic); and 4) highly adapted to rapids habitats but avoiding strong current by burrowing or intrusive behavior (hyporheic). We shall consider the first two categories briefly, and the latter two in more detail.

Poorly adapted

In the poorly adapted category are grouped 32 species; while this represents 24% of the species collected, they comprised only about 2% of the actual number of specimens. Almost half of them are represented by single specimens:

Nannothrissa parva
Hippopotamyrus psittacus
Hippopotamyrus macrops
Marcusenius monteiri
Petrocephalus grandoculis
Alestes liebrechtsii
Hydrocynus lineatus
Hydrocynus goliath
Micralestes acutidens
Citharinus congicus
Citharinus gibbosus
Citharinus macrolepis
Barbus pleuropholis
Labeo lineatus
Labeo velifer
Labeo cyclorhynchus
Labeo weeksii
Auchenoglanis occidentalis
Chrysichthys brevibarbus
Chrysichthys longibarbus
Eutropius grenfelli
Schilbe mystus
Heterobranchus longifilis
Malapterurus electricus
Synodontis alberti
Synodontis notatus
Synodontis pleurops
Synodontis nigriventris
Lates niloticus
Hemichromis bimaculatus
Tylochromis lateralis
Tetraodon mbu.

For all or almost all of these species, presence in the rapids is probably atypical or accidental, and the main populations occur in less turbulent habitats in the mainstream or tributaries. In many instances, they apparently enter becalmed rapids habitats, which they then leave when the water level starts to rise and the current increases. Some of the species in this list were obtained on the margins of rapids habitats, or in less extreme conditions than characteristic of the rapids at high water. It seems unlikely that any of these species establish populations in the more extreme rapids habitats.

Moderately adapted

In this category are grouped 38 species exhibiting little or no morphological adaptation to living in rapids habitats. They are moderately rheophilic or adapted to less extreme rapids habitats; in most instances the main populations occur outside the rapids habitats. They constitute 19% of the specimens collected:

Polypterus ornatipinnis
Microthrissa minuta
Odaxothrissa vittata
Poecilothrissa congica
Potamothrissa acutirostris
Potamothrissa obtusirostris
Mormyrops deliciosus
Mormyrops masuianus
Mormyrus proboscirostris
Mormyrus bumbanus
Petrocephalus simus
Pollimyrus plagiostoma
Alestes macrolepidotus

Alestes imberi
Alestes comptus?
Micralestes humilis
Distichodus mossambicus
Distichodus antonii
Distichodus lusosso
Distichodus sexfasciatus
Distichodus atroventralis
Distichodus fasciolatus
Distichodus maculatus
Barilius weeksii
Barilius lujae
Chelaethiops elongatus
Engraulicypris congicus
Labeo macrostoma
Labeo greenii
Leptocypris modestus
Bagrus ubangensis
Chrysichthys cf. *cranchii*
Synodontis greshoffi
Synodontis caudalis
Synodontis decorus
Synodontis nummifer
Haplochromis polli
Mastacembelus congicus.

The clupeids *Odaxothrissa, Poecilothrissa, Potamothrissa* and *Microthrissa,* along with the cyprinids *Chelaethiops, Engraulicypris,* and *Leptocypris,* apart from their streamlined form and deeply forked caudal fins, exhibit little morphological adaptation to rapids as such; they are basically mid-water or open-water forms often or usually associated with current.

Highly adapted, rheophilic

This is the largest of the four categories, with 51 species and 65% of the specimens. These inhabit the most extreme rapids habitats, and their main populations seem to be restricted entirely or almost entirely to rapids. Many of them exhibit morphological adaptations to the rapids:

Campylomormyrus mirus
Campylomormyrus rhynchophorus
Mormyrops mariae
Mormyrops engystoma
Mormyrus cyaneus
Mormyrus iriodes
Myomyrus macrodon
Myomyrus pharao
Stomatorhinus sp. or spp.
Bryconaethiops yseuxi
Nannocharax macropterus
Garra congoensis
Labeo barbatus
Labeo nasus
Labeo sorex
Labeo variegatus
Labeo lividus
Varicorhinus macrolepidotus
Bagrus caeruleus
Chrysichthys delhezi
Chrysichthys helicophagus
Chrysichthys sp. undet.?
Rheoglanis dendrophorus
Amphilius sp.
Doumea alula
Phractura lindica
Clarias longibarbus
Atopochilus guentheri
Atopochilus royauxi
Chiloglanis congicus
Chiloglanis carnosus
Synodontis acanthomias
Synodontis soloni
Synodontis longirostris
Synodontis brichardi
Haplochromis demeusii
Lamprologus cf. *moquardii*
Lamprologus werneri
Nanochromis consortus
Nanochromis parilus
Nanochromis minor
Nanochromis splendens
Steatocranus gibbiceps
Steatocranus casuarius
Steatocranus tinanti
Steatocranus glaber
Teleogramma gracile
Teleogramma depressum
Mastacembelus cf. *marchei*
Mastacembelus paucispinis
Mastacembelus brachyrhinus.

No fewer than 21 of these are known only from the Zaire River between Kinshasa and

Matadi, and the great majority are apparently restricted to the mainstreams of the Zaire River and of its larger tributaries. Many occur elsewhere in the Zaire basin but not beyond, namely the two *Campylomormyrus, Mormyrops mariae,* the two *Myomyrus, Labeo barbatus, L. sorex, Varicorhinus macrolepidotus, Chrysichthys delhezi, Doumea alula, Phractura lindica, Atopochilus royauxi, Chiloglanis congicus, Synodontis acanthomias, S. longirostris,* and *Lamprologus moquardii.* Several apparently have markedly disjunct distributions, e.g., *L. sorex,* known elsewhere only from the mainstream of the Ubangui River and from the rapids of the Zaire River upstream from Kisangani. A few are relatively rare or only locally abundant in the mainstream rapids but have dense populations in high gradient tributaries such as the Inkisi, especially above waterfalls which act as barriers to the upstream passage of most other fishes. These species are *Garra congoensis, Amphilius* sp., *Doumea alula, Phractura lindica,* and *Chiloglanis congicus.* Our only large mainstream samples of *Amphilius* sp., *Doumea alula,* and *Phractura lindica* came from R & S 41, at a place about on, or two kilometers upstream from the mouth of a large high gradient tributary, the rivière Lufu. The distribution of *Varicorhinus macrolepidotus* is perhaps also affected by the placement of such tributaries.

The commonest readily observable morphological adaptation in the highly specialized rheophilic fishes is reduction of eye size, followed by varying degrees of depression or dorsoventral flattening of the body form. Other adaptations involve modifications of the mouth, fins, and coloration.

Reduction of eye size. Nearly half of the highly specialized rheophilic species are microphthalmic:

Campylomormyrus rhynchophorus
Mormyrops mariae
Mormyrops engystoma
Mormyrus cyaneus
Mormyrus iriodes
Myomyrus macrodon
Myomyrus pharao
Stomatorhinus sp. or spp.
Labeo sorex
Bagrus caeruleus
Chrysichthys sp.
Rheoglanis dendrophorus
Amphilius sp.
Doumea alula
Phractura lindica
Clarias longibarbus
Atopochilus guentheri
Atopochilus royauxi
Chiloglanis congicus
Chiloglanis carnosus
Synodontis acanthomias
Mastacembelus cf. *marchei*
Mastacembelus paucispinis
Mastacembelus brachyrhinus.

The *Mormyrops, Mormyrus, Stomatorhinus,* and *Mastacembelus* belong to genera in which all or almost all species, including those not inhabiting rapids, have small or smallish eyes. In this respect, these genera may be regarded as preadapted to the rapids habitat. The Mormyridae have a complex electrogenic-electrosensory system for gathering information from the environment, and this faculty presumably serves them better than their eyes, in the rapids habitats as well as elsewhere. It should be noted that the reduction of the eye size is more extreme in *Campylomormyrus rhynchophorus, Mormyrus iriodes* and *Stomatorhinus* spp. than in any other Mormyridae. *Labeo sorex, Bagrus caeruleus, Chrysichthys* sp., *Chiloglanis carnosus,* and *Synodontis acanthomias* all have eyes smaller than any or almost any other species in their respective genus. The reduction is particularly striking in *Labeo sorex.* Although the eyes of the rheophilic species listed here are very small, they are always superficial in position, never partially or completely covered by skin and other tissues, and never entirely absent.

Modified body form. A number of the

fishes have dorsoventrally depressed heads and bodies:

Garra congoensis
Bagrus caeruleus
Rheoglanis dendrophorus
Clarias longibarbus
Atopochilus guentheri
Atopochilus royauxi
Chiloglanis carnosus
Synodontis brichardi
Teleogramma depressum.

Chiloglanis carnosus and *Synodontis brichardi,* while not so depressed as most other species listed here, are flatter than any other members of their respective genus. The flattening is most striking in *Atopochilus,* and in *Teleogramma depressum,* which has the flattest head and body of any member of the family Cichlidae (Plate 13, f–g).

A number of the rapids cichlids are exceptionally elongate for members of their family, and this is evidently a modification for life in the rapids:

Lamprologus (three species)
Nanochromis, especially *splendens*
Steatocranus tinanti
Teleogramma, especially *depressum.*

Modifications of the mouth. A number of the rheophilic cyprinids and catfishes belong to genera characterized by highly specialized lips which form a sucking disc:

Garra
Labeo
Atopochilus
Chiloglanis
Synodontis.

Superficially at least, the structure of the sucker in the species inhabiting the rapids of the Lower Zaire River appears to be no more specialized than in species found elsewhere in the Zaire basin or other parts of Africa.

A modification which may have evolved in response to rapids habitats in the Zaire basin is the highly specialized, elongated tubular mouth of *Campylomormyrus.*

Modified fins. A few species have paired fins which are flattened and expanded:

Garra congoensis
Labeo nasus
Labeo sorex
Amphilius sp.
Doumea alula
Phractura lindica.

The three Amphiliidae are most specialized in this respect. None of these species is endemic to the mainstream rapids of the Lower Zair River.

In most cichlids the longest soft ray in the pelvic fin is the first or outermost ray, but in *Steatocranus* and *Teleogramma* it is the third or middle ray, and the first ray is relatively short. This trait is also present in at least some *Lamprologus* species in the rapids, in which the second and third soft pelvic rays are about equally long, and the first ray is shorter.

Coloration. Blue or bluish coloration, evidently an adaptation to the rapids environment, characterizes a surprising number of phyletically diverse rheophilic species:

Mormyrops engystoma uniformly greyish blue
Mormyrus cyaneus uniformly light blue, or light blue with a bluish black head
Labeo nasus dark blue on back and sides, dusky ventrally
Labeo sorex uniformly dusky grey or bluish grey
Labeo lividus dull dark blue on back and sides, lighter ventrally
Varicorhinus macrolepidotus brilliant blue with silvery reflections, white ventrally
Bagrus caeruleus uniformly bluish dorsally and laterally, white ventrally
Chrysichthys delhezi uniformly dark blue dorsally and laterally, whitish ventrally
Chrysichthys helicophagus bluish grey dorsally and laterally, lighter ventrally
Rheoglanis dendrophorus blue or grey-blue dorsally and laterally, greyish ventrally
Atopochilus guentheri mottled with indis-

tinct dark spots; ground color bluish-grey dorsally and laterally, grey or whitish ventrally

Atopochilus royauxi similar to *A. guentheri*, but with a tendency to mottling with smaller spots extending ventrally as well as dorsally and laterally.

Chiloglanis carnosus light bluish with violet undertones on back and sides, lightening ventrally; a pair of dorsolateral white spots just in front of adipose fin, and a somewhat smaller pair just in back of adipose fin (Plate 8, b).

Synodontis acanthomias small, roundish dark spots on a whitish, grey, or bluish grey background, lightening ventrally

Mastacembelus paucispinis young mottled; adults uniformly bluish, or bluish with violaceous undertones.

In other riverine habitats in the Zaire basin, relatively few species exhibit blue or bluish coloration, indicating strong selection for such coloration in the rapids. There is some indication that it is involved in concealment. Many of the fishes, as indicated above, are lighter ventrally (countershaded), as in classical cases of blending or concealing coloration exhibited by fishes in a great variety of environments. The mottling of the two species of *Atopochilus* definitely helps to conceal them from human observation, and their bluish coloration appears to complement this effect. *Atopochilus* provides perhaps the best examples of concealing coloration among the rapids fishes.

At least two species of Mormyridae are characterized by darkly pigmented (Black) and depigmented (White) phena or morphs: *Mormyrops mariae* (Plate 5, a-b) and *Stomatorhinus* sp.

Highly adapted, intrusive or hyporheic

This fourth category, our last, comprises only eight species, all highly specialized and apparently endemic to the rapids of the Lower Zaire River. They account for 14% of the specimens taken by our survey:

Notoglanidum pallidum
Gymnallabes tihoni
Gymnallabes nops
Lamprologus lethops
Mastacembelus brichardi
Mastacembelus crassus
Mastacembelus latens
Mastacembelus aviceps.

Of these species, *Mastacembelus brichardi* and *Gymnallabes tihoni* appear to be the most abundant. *M. brichardi* occurred at six of our nine rapids collecting localities, and was very abundant at four of them. *G. tihoni* was present at four localities, and was so abundant at R & S 41 that we had to discard two or three hundred, which are not included in our tallies. *Mastacembelus crassus* was abundant only at one locality, R & S 29, in the same rocky pool that yielded our only specimens of *Lamprologus lethops* and *M. latens*. Of the approximately 750 specimens taken from this pool, 45% belong to our hyporheic category.

Notoglanidium pallidum and *Mastacembelus aviceps* are microphthalmic, and *Gymnallabes nops* apparently anophthalmic (we have not dissected the head of the unique specimen to verify this point). The remaining species are cryptophthalmic. In *Gymnallabes tihoni* and *Mastacembelus crassus* the eyes lie in little pits or crypts, largely hidden from the surface; in *Lamprologus lethops, Mastacembelus brichardi,* and *M. latens* they are completely covered over by the skin and tissues of the head. We suspect these species employ the eyes primarily to detect light, from which they flee.

In *Mastacembelus brichardi* and *latens* the head and body are laterally compressed, of a form more or less typical of *Mastacembelus* from non-rapids habitats. In *Notoglanidium pallidum* and *Gymnallabes tihoni* the head and body are strongly depressed, as in some of the highly rheophilic forms. The heads and bodies of *Gymnallabes nops, Lamprologus lethops, Mastacembelus crassus,* and *M. aviceps,* on the other hand, are more or less of uniform

thickness and round in cross-section, a form rarely encountered in riverine fishes, and absent among the rheophilic forms from the Lower Zaire rapids. Perhaps these hyporheic species with round bodies burrow into the mud (*Gymnallabes nops, Mastacembelus aviceps*) or loose rock rubble (*Mastacembelus crassus, Lamprologus lethops*?) that accumulate underneath and between rocks in the rapids.

DISCUSSION

Speciation and adaptation in the extensive tracts of rapids habitats in the mainstream of the Zaire River and its larger tributaries has contributed significantly to the present diversity of the rich and highly endemic Zairean ichthyofauna. The families most strongly affected by this evolution have been Mormyridae, Bagridae, Mochokidae, and Cichlidae, but its effect has been felt to some extent by at least five more of the 25 families inhabiting the Zaire basin: Cyprinidae, Amphiliidae, Clariidae, Characidae, Schilbeidae and Mastacembelidae.

Rapids fishes in the Zaire basin are still far from being well known, especially those of the Ubangui, the Kasai, and the Upper Zaire River or Lualaba. A number of species found to be relatively common by our survey of the Lower Zaire rapids were previously known from only the holotypes or a few specimens, with little or no precise indication of habitat: *Mormyrops engystoma, Bryconaethiops yseuxi, Labeo sorex, Chrysichthys delhezi, Clarias longibarbus, Teleogramma gracile, Mastacembelus paucispinis,* and *M. brachyrhinus.* It is likely that additional distinctive but poorly known species will prove to be fairly common in rapids.

The familial composition of the rapids fishes obtained by us in the Lower Zaire River is indicated in Table 22. It is a remarkable fact that cichlids are represented by more than twice as many endemic rapids species as any other family, and that these endemic cichlid species together constitute more than one-third of the total number of specimens collected! This contrasts very sharply indeed with rich riverine faunas elsewhere in Africa, particularly the Cuvette Central of Zaire (the richest area), where cichlid species are invariably few and seldom constitute a major portion of the individual fishes present. The one place in the Zaire basin where cichlid predominance surpasses that of the rapids is Lake Tanganyika. This invites a comparison of the rapids fauna with that of the lake. The spectacular success of Cichlidae in the great lakes of East Africa has been the subject of much good evolutionary speculation (Fryer and Iles, 1972; Greenwood, 1974), but far less attention has been given to other fish groups and to the great riverine fish faunas of Africa.

Table 22. The families and the numbers of specimens, genera, species, and endemic species taken at nine collecting localities in rapids habitats in the mainstream of the Lower Zaire River.

	Specimens	Genera	Species	Endemic Species
1. Cichlidae	2694	7	17	13
2. Mormyridae	1042	8	19	3
3. Mastacembelidae	905	1	8	6
4. Cyprinidae	648	8	19	2
5. Mochokidae	552	3	16	3
6. Clupeidae	357	5	6	0
7. Bagridae	240	5	11	4
8. Amphiliidae	214	3	3	0
9. Clariidae	181	3	4	2
10. Distichodontidae	146	2	8	0
11. Characidae	124	4	9	1
12. Citharinidae	14	1	3	0
13. Malapteruridae	14	1	1	0
14. Schilbeidae	10	2	2	0
15. Polypteridae	6	1	1	0
16. Tetraodontidae	1	1	1	0
17. Centropomidae	1	1	1	0
Totals	7149	56	129	34

Table 23. Fish families of the Zaire basin and their contribution to the fauna of Lake Tanganyika and of the Lower Zaire rapids.

	Present		Endemics	
	Lake	Rapids	Lake	Rapids
Lepidosirenidae	+*			
Polypteridae	+	+		
Clupeidae	+	+	+	
Mormyridae	+	+		+
Pantodontidae				
Kneriidae				
Phractolaemidae				
Characidae	+	+	+	+
Distichodontidae	+	+		
Citharinidae	+	+		
Ichthyboridae				
Cyprinidae	+	+	+	+
Bagridae	+	+	+	+
Schilbeidae		+		
Amphiliidae		+		+
Clariidae	+	+	+	+
Mochokidae	+	+	+	+
Malapteruridae	+	+		
Cyprinodontidae	+		+	
Centropomidae	+	+*	+	
Anabantidae	+*			
Eleotridae				
Cichlidae	+	+	+	+
Mastacembelidae	+	+	+	+
Tetraodontidae	+	+*		

* Presence marginal.

Of the three African lakes in which explosive lacustrine evolution has produced large numbers of endemic species, Tanganyika has a far greater number of endemic genera (43) than Malawi and Victoria combined (28). The explanation most often advanced for this difference is the time factor, Tanganyika being several million years older than Malawi and Victoria. As pointed out by Roberts (in press), the explanation should also be sought in the relatively impoverished riverine faunas from which the Malawi and Victoria ichthyofaunas evolved. The greater diversity of the Tanganyika ichthyofauna must be related in part to the rich Zairean stocks which contributed to it. As indicated in Table 23, seven of the ten families which have contributed endemics to the Tanganyikan fauna are also represented by endemics in the rapids of the Lower Zaire River. It seems a reasonable hypothesis that evolution in the rocky habitats in the rapids of the Zaire basin played a major role in preadapting such families as Cichlidae, Mastacembelidae, Mochokidae, Clariidae, Bagridae, and Cyprinidae to the rocky littoral of Tanganyika, with pride of place to the endemic Zairean cichlid genus *Lamprologus*.

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Evolution of the Scale-Eating Cichlid Fishes of Lake Tanganyika: A Generic Revision with a Description of a New Species

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EVOLUTION OF THE SCALE-EATING CICHLID FISHES OF LAKE TANGANYIKA: A GENERIC REVISION WITH A DESCRIPTION OF A NEW SPECIES

KAREL F. LIEM[1] AND DONALD J. STEWART[2]

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ABSTRACT. A new scale-eating cichlid, *Perissodus eccentricus*, from Lake Tanganyika has been discovered, differing from all other lepidophagous Tanganyikan cichlids in its asymmetrically suspended jaws, low dorsal spine count and asymmetrically arranged jaw teeth. All lepidophagous cichlid species of Lake Tanganyika share a unique combination of one dental, one neurocranial, three mandibular, one maxillary, one palatal, and one branchial specializations. Because of a basic homogeneity in its specialized and unique morphology, the lepidophagous assemblage is considered monophyletic with all constituent species classified into one single genus, *Perissodus*. On phylogenetic grounds, it is proposed that *Plecodus* and *Xenochromis* be regarded as invalid genera. All specializations are adaptive integrations of structural elements to provide: a powerful and stable jaw closing mechanism; a capacity to open the mouth widely; highly mobile upper pharyngeal jaws which, in close coordination with the lower pharyngeal jaw, can arrange scales into manageable packets prior to deglutition. Interspecific relationships have been established on the basis of shared specializations in dentition, osteology and myology. Within the lineage we can detect an evolutionary trend towards occupation of progressively narrower adaptive zones. The simple morphogenetic mechanisms underlying this pronounced asymmetry are bilateral differences in differential growth rates of two bones in the jaw suspension and the remodeling of articular surfaces of the lower jaw joints. It is suggested that the anatomy of the new species, with its asymmetrical jaw suspension, furnishes further evidence that the underlying evolutionary mechanism involved in the explosive radiation of lacustrine cichlids is differential growth in various skull-elements.

INTRODUCTION

Lepidophagous cichlid fishes endemic to Lake Tanganyika are thought to be of diphyletic origin (Regan, 1920; Poll, 1950, 1956). Within the diphyletic pattern, *Perissodus microlepis* Boulenger 1898, represents a specialized monotypic genus with a pharyngeal apophysis composed of the parasphenoid only. Such a simple composition of the pharyngeal apophysis has been regarded as an indicator of phyletic origin from a *Tilapia*-like ancestor. In contrast, all species of the genus *Pleco-*

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dus (*sensu* Boulenger, 1898) and *Xenochromis* (*sensu* Boulenger, 1899) possess a pharyngeal apophysis to which both the parasphenoid and basioccipital contribute, allegedly reflecting phyletic affinity with the genus *Haplochromis*. Wickler (1963) and Fryer and Iles (1972) have challenged the validity of using these two character states of the pharyngeal apophysis in establishing phyletic relationships within the family Cichlidae. In some species we have observed that the inclusion of the basioccipital in the apophysis is variable to such an extent that left and right sides of an individual specimen may differ. So far we have failed to determine which of the two character states represents the derived condition. This makes it virtually impossible to use the anatomy of the apophysis meaningfully in our phyletic analysis. Because of the paucity of evolutionary data on the various characters, the phyletic pattern of lepidophagous cichlids of Lake Tanganyika as conceived by Regan (1920) remains open to alternative interpretations.

The discovery of a new species of scale-eating cichlid with either sinistral or dextral asymmetry of the jaw teeth and representing a deep-water counterpart of *P. microlepis* has shed new light on the evolutionary mechanism underlying the adaptations to scale-eating. Jaw dentition of the juvenile of the new form is asymmetrical as in adults, but the anterior mandibular teeth are of the specialized form characterizing *Perissodus* (*sensu* Boulenger) whereas the form of the lateral premaxillary teeth is typical for *Plecodus* (*sensu* Boulenger). Subsequent analysis of jaw dentition of all scale-eating cichlids of Lake Tanganyika has revealed that the jaw teeth of *P. microlepis* are not unique, but are, in fact, characteristic of the group as a whole, encompassing all known species of *Perissodus*, *Plecodus* and *Xenochromis*.

In this study, we will attempt the following: (1) to offer an anatomical profile of the new species since it exhibits key phylogenetic characters for all lepidophagous cichlids of Lake Tanganyika; (2) to analyze comparative and functional aspects of the osteology and myology of all species within the lepidophagous group; (3) to determine the interrelationships within this trophic group and to offer a generic revision; and (4) to discuss the possible evolutionary pathway leading to the unique asymmetry in the new species.

MATERIALS AND METHODS

Proportional measurements and meristic counts are essentially those used by Thys van den Audenaerde (1964). The extent to which the last soft dorsal and anal fin-ray elements were separated from their preceding element was variable; counts presented (see Table 2) are for all elements irrespective of whether or not the last two are joined at the base. Measurements are taken to the nearest 0.1 mm.

The specimens listed below have been examined from the following institutions: British Museum of Natural History (BMNH), Museum of Comparative Zoology (MCZ), Tervuren Museum, Belgium (TM), University of Michigan Museum of Zoology (UMMZ), and United States National Museum (USNM):

Perissodus eccentricus sp. n.: UMMZ 196003, 196004, 196056, 196005, 196006; MCZ 50092, 50093; TM 74–27–P–1; BMNH 1975.1.28:1.

Perissodus microlepis Boulenger: BMNH 1898 9.9.61 (holotype), 1960 9.30.6388–6391; MCZ 49332; UMMZ 196000, 196002, 196001.

Perissodus burgeoni David: TM 38892–38896 (types).

Perissodus gracilis Myers: USNM 102111 (paratypes).

Plecodus paradoxus Boulenger: BM 1960 9.30.6468–6482; MCZ 49330.

Plecodus straeleni Poll: MCZ 49328.

Plecodus multidentatus Poll: BM 1960 9.30.60528–60529 (paratypes); MCZ 49543, 49544, 49545.

Plecodus elaviae Poll: MCZ 49331.

Xenochromis hecqui Boulenger: BM 692,

Table 1. Morphometric characteristics in per mille standard length or per mille head length (*) of *P. microlepis* and the type series of *P. eccentricus*.

Character	*eccentricus*		*microlepis*		
	Holotype	Holotype and 14 paratypes	Holotype	*P. gracilis*, 2 paratypes	7 specimens from Zambia
Total length, mm	164	81–164	95		
Standard length, mm	128	64–128	81	46– 54	55–103
Body depth	289	257–289	247	243–249	255–287
Head length	305	293–334	288	306–356	289–310
Caudal pedunele length,	198	163–202	177	178–180	161–172
least depth	105	104–115	121	102–108	106–117
Last dorsal spine length	130	124–145	109	114	110–126
Third anal spine length	138	136–166	105	106–117	110–129
Pectoral length	284	264–293			
Pelvic length	250	244–285			
Orbit diameter*	349	315–373	290	299–315	256–304
Interorbital bony width*	256	240–267	298	213–248	247–315
Snout length*	295	278–307	274	335–382	298–356
Preorbital depth*	82	66– 90	95	55– 60	63– 91
Premaxillary pedicle length*	210	191–210	179	171–182	157–203
Mandible length*	385	299–385	369	317–339	305–343

1960 9.30.6364–6369, 1960 9.30.6381–6386, 1950 4.1.5097–5103, 1960 9.30.6370–6373, 1960 9.30.6376–6380; MCZ 49333, 49334.

With a few exceptions, osteological and myological nomenclature follows that of Liem (1970), and Winterbottom (1974), respectively.

Scanning electron micrographs are based on excised jaws which have been cleaned with diluted solutions of sodium hypochlorite, dehydrated in absolute alcohol, mounted with silverpaint and coated with gold.

Perissodus eccentricus new species
Figure 1, Tables 1 and 2

Holotypes: UMMZ 196003, 128 mm (164 mm TL); Paratypes· UMMZ 196004, 3:102–121 mm; UMMZ 196056, 5:109–117 mm; UMMZ 196005, 2:92–94 mm; UMMZ 196006, 2:86–88mm; BMNH, 1975.1.28:1:1:91 mm; MCZ 50093, 1:121 mm; MCZ 50092, 1:92 mm (alizarin prep.); MCZ 50718, 1·63.5 mm (formerly TM 112610); TM 74–27–P–1, 1:122 mm.

Description. Differs from other lepidophagous Tanganyikan cichlids by its asymmetrical jaw teeth and low dorsal spine count (14–15 cf. 16–20). Jaws suspended asymmetrically in such a way that a given individual can only use one side of its mouth to bite scales from prey. Dextral-jawed specimens have left side of most teeth of both the upper and lower jaws abraded at an angle and variously slanting laterally to the right; right side of mandible is lower and jaws project to the right when opened (Plates 1, 2, Figs. 17–22). Sinistral- and dextral-jawed specimens are equally abundant. Two specimens had a row of 11–16 pored scales above the upper lateral line and contiguous with the base of the soft dorsal fin. Such an elaboration of the lateral line has not been reported for any cichlid to our knowledge.

P. eccentricus is closely allied to *P. microlepis* from which it differs further as follows: (1) has more upper and lower lateral line pores, upper lateral line extends posteriorly beyond end of dorsal fin base (cf. not beyond end) and lower lateral line extends forward to tip of pectoral fin (cf. not reaching pectoral fin); (2) has longer last dorsal and anal spines; (3) has larger orbits; when comparing similar sized specimens, orbit (as a percentage of head length) provides a 100% dichotomy but because of negative allometry of orbit

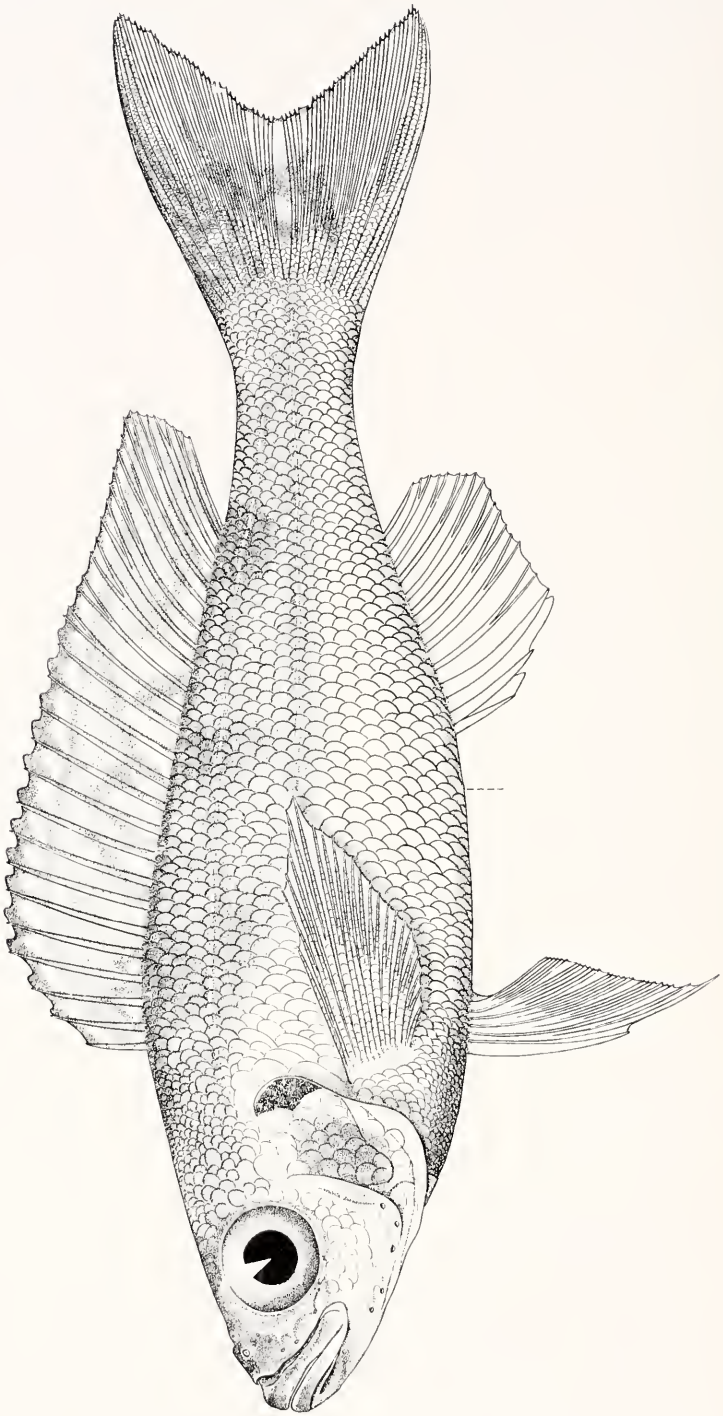

TABLE 2. MERISTIC CHARACTERISTICS OF *P. MICROLEPIS* AND THE TYPE SERIES OF *P. ECCENTRICUS*.

Character	*eccentricus*		*microlepis*		
	Holotype	Holotype and 14 paratypes	Holotype*	*P. gracilis*, 2 paratypes	7 specimens from Zambia
Dorsal fin spines,	XIV	XIV–XV	XVIII	XVII	XVII–XVIII
rays	11	10–13	11(10)	11–12	10–11
Anal fin	III, 9	III, 9–11	III, 9(8)	III, 9–10	III, 9–11
Upper lateral line scales	57	51–60	47(44)	45–46	44–51
Lower lateral line scales	37	32–45	31	21–25	25–31
Lateral line scales	64	63–69	65	67	62–70
Transverse scale rows	5.5/18	5.5–7/16–18	(5/20)		
Cheek scale rows	3	2–3	(3)	3	3
Circumpedunclar scales	27	27–31	30	28–29	29–30
Premaxillary teeth	23	20–24	23(20)	19–22	20–27
Mandibular teeth	17	14–18	19(18)	16	16–21
Gillrakers	17+1+5	(16–19)+1+(4–6)	18+1+7(14)	(19–20)+1+7	(18–20)+1+(6–7)
Vertebrae	15+18				

* Numbers in brackets are from original description by Boulenger (1898).

juvenile *P. microlepis* (< 50 mm) may have orbits as large as adult *P. eccentricus* (> 110 mm); (4) has terminal mouth (cf. superior mouth and projecting mandible); (5) has weakly developed melanophores on head and body; in preserved specimens, pelvic and anal fins clear, dorsal and caudal fin with faint grey mottlings (Figure 1). This is in sharp contrast to *P. microlepis* which usually has pelvic and vertical fins, head and body heavily pigmented, dark olive-brown in alcohol. Relatively large eyes and perhaps also the extended lateral line pores of *P. eccentricus* are believed to be sensory compensations for life in a dim habitat.

No obvious sexual dimorphism or dichromatism in preserved specimens; life colors are unknown.

The type series for *P. burgeoni* David 1936 and paratypes of *P. gracilis* Myers 1936 (Tables 1 and 2) were re-examined to be sure *P. eccentricus* was not involved. With respect to diagnostic characters mentioned above, all specimens agreed with *P. microlepis;* we concur with Poll (1946, 1956) in synonymizing these taxa with *P. microlepis.*

Etymology. Eccentricus, from Greek *ekkentros,* from *ex* (out of) + *kentron* (center). This name seems appropriate as it alludes to asymmetry of the teeth and jaws as well as the strange or unconventional morphology and inferred feeding behavior.

Food habits. All stomachs of *P. eccentricus* which were not empty contained only fish scales most or all of which were from cichlids. As all specimens except the one juvenile were taken in deep-water gill nets, our analysis of food habits could be biased against rapidly digested items.

Distribution. Endemic to Lake Tanganyika; adults known only from 60–100 m depths in Zambia—Musende Bay, Chituta Bay and off Mwela; one juvenile collected in a trawl 5 km east of Kalemié (formerly Albertville), Republique du Zaire at 70–100 m. Depth distribution is complementary to that of *P. microlepis* which is abundant in water less than 15 m deep and has a maximum verified depth range to 40 m (Poll 1956).

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Figure 1. *Perissodus eccentricus*, holotype, UMMZ 196003, male, Chituta Bay, 100 m, Lake Tanganyika, Zambia. Lateral view. (Drawn by Patricia Chaudhuri.)

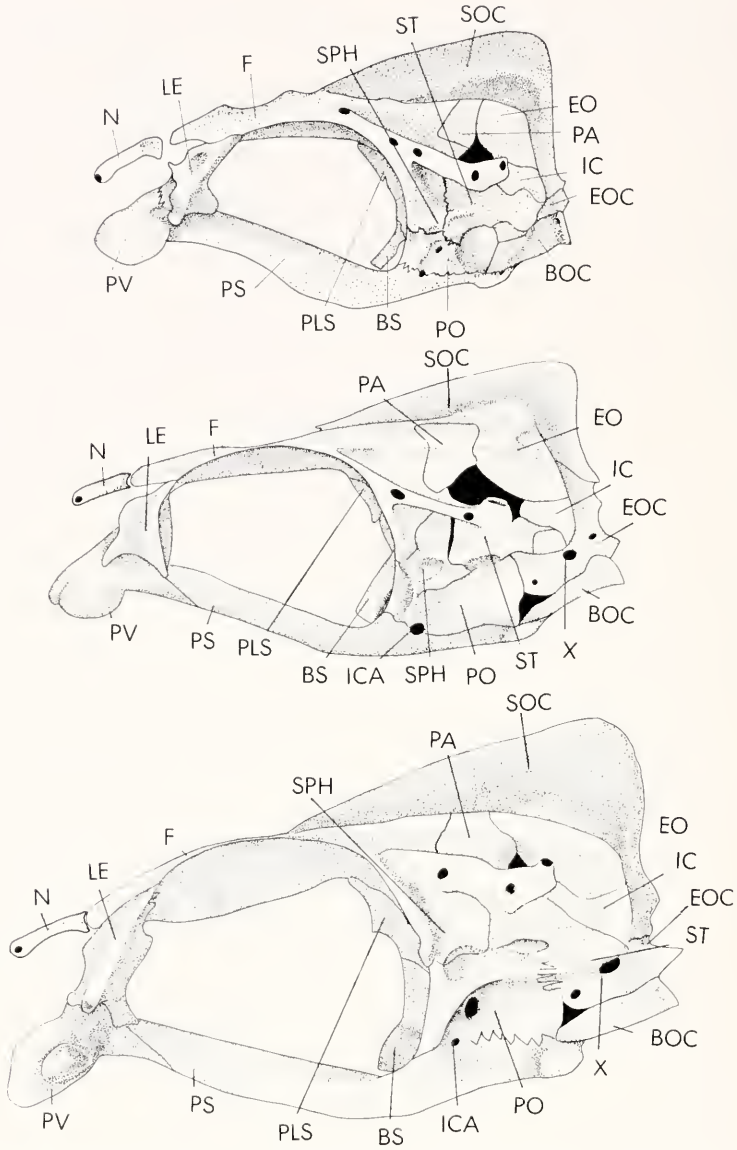

Figure 2. Lateral aspect of neurocranium. A, *eccentricus*; B, *microlepis*; C, *hecqui*.

SOME OSTEOLOGICAL ASPECTS OF *P. ECCENTRICUS*

Neurocranium

The marked asymmetry of the suspensory apparatus has not affected the bilateral symmetry of the neurocranium.

The roof of the neurocranium (Fig. 4A) conforms to that of more generalized cichlids as described by Greenwood (1967, 1974), Vandewalle (1972) and Goedel (1974a, b). However, several distinguishing features can be recognized in *P. eccentricus*. Anteromedially the cranial roof possesses a shallow and rather restricted rostral fossa the floor of which is

made up solely by the ethmoid (Fig. 4A: E, PV, F). In the ethmoid region, there is a sutural junction between ascending processes of the vomer with the lateral ethmoid. Very restricted connections are present between the ethmoid and ascending processes of the vomer (PV).

Although highly specialized in some features, the neurocranium of *P. eccentricus* retains such primitive characteristics as the

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KEY TO ABBREVIATIONS

A:	articular
A_1:	adductor mandibulae pars A_1
A_2:	adductor mandibulae pars A_2
AAP:	adductor arcus palatini
AD:	adductor branchialis
ADA:	ascending process of articular
AM_1:	adductor mandibulae pars A_1
AM_2:	adductor mandibulae pars A_2
AM_3:	adductor mandibulae pars A_3
AO:	adductor operculi
AP:	articular process
APA:	ascending process of articular
APD:	ascending process of dentary (coronoid)
APPM:	ascending process of premaxilla
BL:	Baudelot's ligament
BOC:	basioccipital
BS:	basisphenoid
BSR:	branchiostegal ray
CB:	ceratobranchial
CB_5:	fifth ceratobranchial (lower pharyngeal jaw)
CC:	cranial condyle
CL:	cleithrum
D:	dentary
DO:	dilatator operculi
E:	ethmoid
EB:	epibranchial
ECT:	ectopterygoid
ENT:	entopterygoid
EO:	epiotic
EOC:	exoccipital
EP:	epaxial muscles
ES:	esophagus
F:	frontal
GHA:	geniohyoideus anterior
GHP:	geniohyoideus posterior
HH:	hyohyoideus
HHI:	hyohyoideus inferior
HHS:	hyohyoideus superior
HM:	hyomandibula
HY:	hyoid
IAM_{1-2}:	intramandibularis 1 and 2
IC:	intercalary
ICA:	foramen for internal carotid artery
IML:	interoperculomandibular ligament
IOP:	interoperculum
L:	ligament
LAP:	levator arcus palatini
LE:	lateral ethmoid-prefrontal complex
LE_4:	fourth levator externus
LEM:	levator externus muscle
LI:	levator internus
LIM:	interoperculomandibular ligament
LO:	levator operculi
LP:	levator posterior
M:	mandible
MD:	mandible
MMM:	collagen tract within lower lip
MPT:	metapterygoid
MX:	maxilla
N:	nasal
OD:	obliquus dorsalis
OF:	obliquus posterior
OP:	operculum
P:	palatine
PA:	parietal
PB_1:	first pharyngobranchial
PC:	premaxillary condyle
PCE:	pharyngocleithralis externus
PCI:	pharyngocleithralis internus
PF:	prefrontal-lateral ethmoid complex
PHH:	rectus communis (pharyngohyoideus)
PLS:	pleurosphenoid (pterosphenoid, alisphenoid)
PM:	premaxilla
PO:	prootic
POP:	preoperculum
PP:	postmaxillary process of maxilla
PPM:	protractor pectoralis
PS:	parasphenoid
PV:	vomer
Q:	quadrate
RP:	retractor dorsalis (retractor ossium pharyngealium)
SCL:	supracleithrum
SH:	sternohyoideus
SOC:	supraoccipital
SOP:	suboperculum
SPH:	sphenotic
ST:	pterotic (supratemporal)
SY:	symplectic
TAM:	tendon of adductor mandibulae
TDA:	transversus dorsalis anterior
TDA_{1-3}:	transversus dorsalis anterior parts 1–3
TDP:	transversus dorsalis posterior
UH:	urohyal
V:	vertebra
X:	foramen of vagus nerve

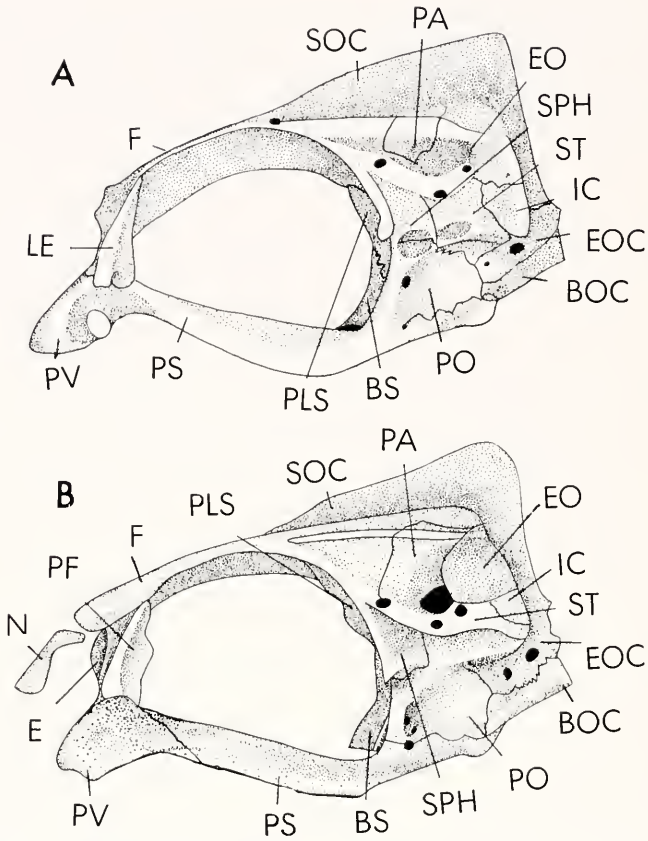

Figure 3. Lateral aspect of neurocranium. A, *multidentatus*; B, *paradoxus*.

somewhat decurved dorsal profile to the preorbital face, the high cranial vault and the relatively short ethmovomerine region (Fig. 2A). At the orbital level, the parasphenoid turns dorsally to join the ethmovomerine complex giving the cranial base a pronounced curved profile. Posteriorly the long axis of the basioccipital makes a 25 degree angle with the horizontal plane. The relatively small pharyngeal apophysis is formed from the parasphenoid only.

Suspensory Apparatus

Bilateral asymmetry is especially pronounced in the anterior part of the suspensory unit, the posterior half being symmetrical.

In dextral individuals the right palatine-maxillary joint is located more posteriorly and laterally than the left joint (Fig. 15A). The depth of the suspensory apparatus measured from the dorsal rim of the body of the palatine to the ventral edge of the condyle of the quadrate is much greater on the left side (Fig. 15C) in dextral individuals. Consequently, the quadrato-mandibular joint in dextral individuals is positioned more dorsally on the right side (Fig. 15B, C).

The suspensory apparatus in dextral individuals is distinctly longer on the left side when measured between the anterior tip of the maxillary process of the palatine and the anterior edge of the anterior head of the hyomandibular. Yet the left and right palatines and hyomandibulars exhibit

identical proportions and shapes. Asymmetry appears to have arisen by differences in orientation and proportions of the quadrate-symplectic complex. Dextral individuals possess a more horizontal and relatively shorter symplectic and an anteriorly rotated quadrate on the right side. Unlike the right one, the left quadrate has a vertically orientated cranial border (Fig. 16).

Exceptionally strong sutural connections between the symplectic process of the hyomandibular, metapterygoid, entopterygoid, and palatine bones may add strength to the suspensory apparatus, which must be able to absorb considerable forces during the "bite." Additional adaptations to withstand exceptionally strong forces have evolved in the head of the palatine which is firmly anchored to the vomer and prefrontal by unusually well-developed processes. The metapterygoid and entopterygoid are enlarged, forming mediodorsally directed shelflike extensions partially bridging the gap between the parasphenoid and the suspensory apparatus. A well-developed adductor fossa in the preoperculum accommodates the A_2 and A_3 parts of the adductor mandibulae muscle (Fig. 5A POP).

Jaw Apparatus

Asymmetry is especially evident during opening and protrusion of the jaws. Both upper and lower jaws deviate either to the left or right side respectively in sinistral and dextral individuals. However, no asymmetrical features have been found between left and right sides of the premaxillae, maxillae and dentaries. Noticeably asymmetrical differences in the mandible are confined to the left and right articulars.

In the mandible, the extraordinarily well-differentiated dentary has become by far the most dominant component, occupying almost the entire length of the dorsal mar-

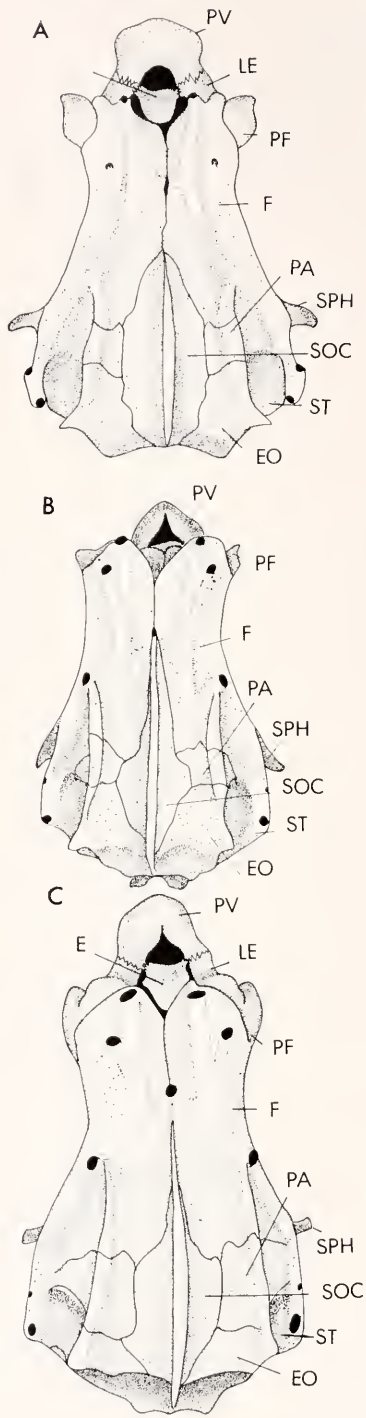

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Figure 4. Dorsal aspect of neurocranium. A, *eccentricus*; B, *paradoxus*; C, *microlepis*.

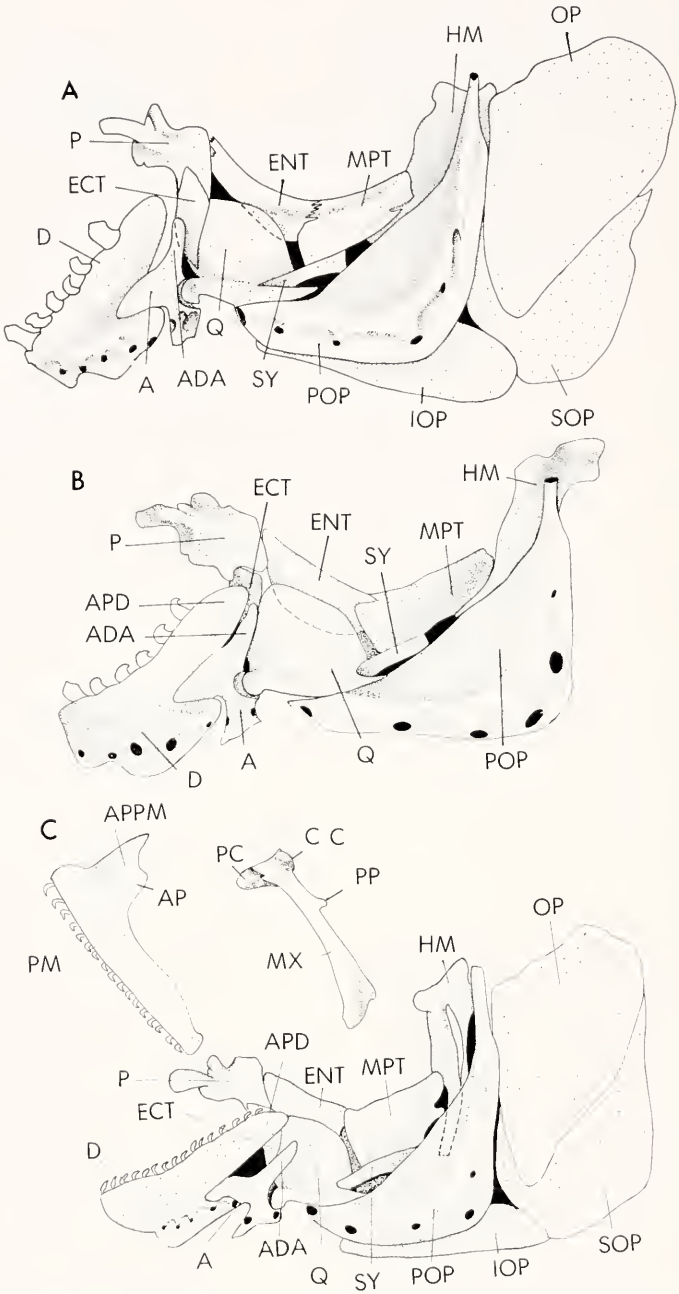


Figure 5. Lateral aspect of suspensory apparatus and mandible. A, *eccentricus*, opercular apparatus included; B, *microlepis*; C, *multidentatus*, opercular apparatus and upper jaw included.

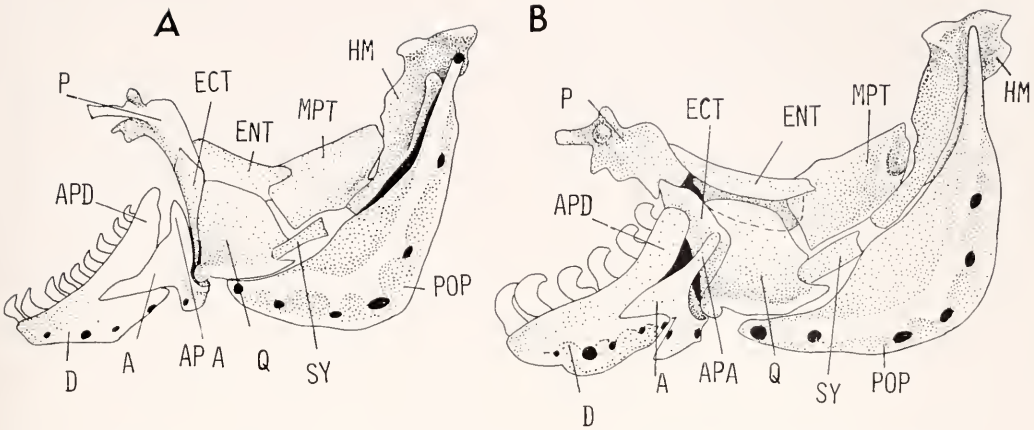


Figure 6. Lateral aspect of suspensory apparatus and mandible. A, *hecqui*; B, *paradoxus*.

gin and forming about 70 percent of the total mandibular length ventrally. A deep notch in the ventral margin of the dentary at the level of the second mandibular pore gives the mandible a characteristic lateral profile (Fig. 5A:D). The most outstanding mandibular feature is the topography of the ascending process of the dentary, which reaches dorsally to the middle of the maxilla when the jaws are fully opened. Compared with the dentary, the articular is small, although it possesses a high slender ascending process. In dextral individuals, the articulatory surface of the right articular socket is deeper and more nearly U-shaped in lateral view compared with the left articular (Fig. 16). The articulatory head of the right quadrate is smaller and directed more anteriorly in dextral individuals, while that of the left quadrate is larger and directed more ventrally.

The premaxilla has a very long alveolar process while the ascending process is exceptionally short and slender. Flanking the ascending process is a prominent articular process (Fig. 7A:AP, APPM).

The maxilla is distinctly elongate and rather slender with a concave anterior margin. Ventrally the body of the maxilla ends in a slender process. Originating from the posterior margin slightly above the middle of the maxillary body is a characteristically well-developed process hence called the postmaxillary process (Fig. 7A: PP). The premaxillary condyle is long and stout and originates from the body of the maxilla at an angle of about 30 degrees. The proximal tip of the maxillary body is blunt and abbreviated.

MYOLOGICAL ASPECTS OF *P. ECCENTRICUS*

Although the adductor-mandibulae complex conforms to that of other cichlids as described by Vandewalle (1972), Goedel (1974a, b), and Liem and Osse (1975), four important specializations (Fig. 8A) have evolved in *P. eccentricus*: (1) The adductor mandibulae pars A_2 is clearly subdivided into a dorsal head which inserts on the ascending (coronoid) process of the dentary by means of an aponeurosis passing medially to the ascending process of the articular (cf. Goedel, 1974a, who illustrates a lateral passage in Fig. 18b but describes a medial topography on p. 258). The ventral head, originating mainly from the horizontal limb of the preopercular and symplectic, inserts via an aponeurosis on the posterior aspect of the slender ascending process of the articular (Fig. 10A); (2) Pars A_3 of the adductor mandibulae complex is greatly reduced although it maintains the same topography as in

Tilapia; (3) A considerable shortening in relative length of the muscle fibers of the adductor arcus palatini has accompanied the approximation of the dorsal rim of the suspensory apparatus and the parasphenoid. Concomitant with fiber length shortening, both the anterior and posterior extents of the adductor arcus palatini have been reduced; (4) The intramandibular division of the adductor complex (m. mentalis of Goedel, 1974a, b; the quadrato-dentaire of Vandewalle, 1972) is distinctly differentiated into two independent entities (Fig. 10B). One dorsal subdivision represents the original intramandibularis muscle ($Aw = IAM_1$) retaining the typical topography. The larger, more ventral subdivision (IAM_2) includes a strong tendon beginning at the medial aspect of the quadrate at the quadratomandibular joint level and inserting on the entire medial surface of the mandible ventral to the dorsal part of the intramandibularis muscle. Goedel (1974a, b) does not mention such a subdivision in *Tilapia tholloni*, but Vandewalle has recorded the presence of a separate head ("muscle quadrato-dentaire") in *Tilapia guineensis*.

The hyoid and opercular musculature in *P. eccentricus* conform with generalized cichlids in the levator arcus palatini (LAP), dilatator operculi (DO), levator operculi (LO), adductor operculi, adductor hyomandibulae and adductor operculi muscles (Fig. 8A). However, the geniohyoideus anterior and posterior in *P. eccentricus* (Fig. 11) form a much more elongate compound muscle with two distinct tendinous inscriptions, indicating a capability to produce greater excursions of the hyoid apparatus and mandible. The hyohyoideus superior and inferior and the sternohyoideus (Fig. 11:HHS, HHI, SH) exhibit the same topography and morphology found in generalized cichlids. Such a retention of a basic integration of the hyoid and branchiostegal elements may be correlated with the exceptional efficiency of this functional complex in respiration. In *P. eccentricus* the hyohyoideus inferior is greatly reduced.

Although the branchial and pharyngeal muscles in *P. eccentricus* do not deviate much from those found in the characteristic cichlid body plan as described by Liem (1973), and Liem and Osse (1975), some salient specializations have been found. The transversus dorsalis anterior is greatly reduced with the total loss of one head, while the second and third heads are rudimentary. The third head has lost its connections to the parasphenoid (Fig. 13A:TDA). Although still relatively well-differentiated, the transversus dorsalis posterior (Fig. 13A:TDP) has undergone marked reduction compared with the condition in generalized cichlids. Marked hypertrophy of the first levator internus (Fig. 13A:LI) gives the branchial musculature a unique appearance. The second levator internus has remained unmodified. The rectus communis (pharyngohyoideus) is very prominent ventrally both in length and cross section (Fig. 12A:PHH). A tendon divides the rectus communis into two distinct bellies. The pharyngocleithralis externus, a functional antagonist of the rectus communis, has also undergone significant hypertrophy (Fig. 12A:PCI). As in all cichlids, the fourth levator externus is composed of a rudimentary lateral head inserting on the dorsal aspect of the fourth epibranchial by means of an aponeurosis, whereas the dominant medial head (identified by Goedel, 1974 [a, b] as a protractor arcuum branchialium, a *de novo* muscle development) inserts on the muscular process of the lower pharyngeal jaw.

COMPARATIVE ANATOMY OF THE SCALE-EATING GROUP

Having outlined the main morphological features of this highly specialized new species, we can consider the anatomy of all other lepidophagous cichlids of Lake Tanganyika, grouped into three separate genera by previous authors:

Xenochromis Boulenger 1899 has been

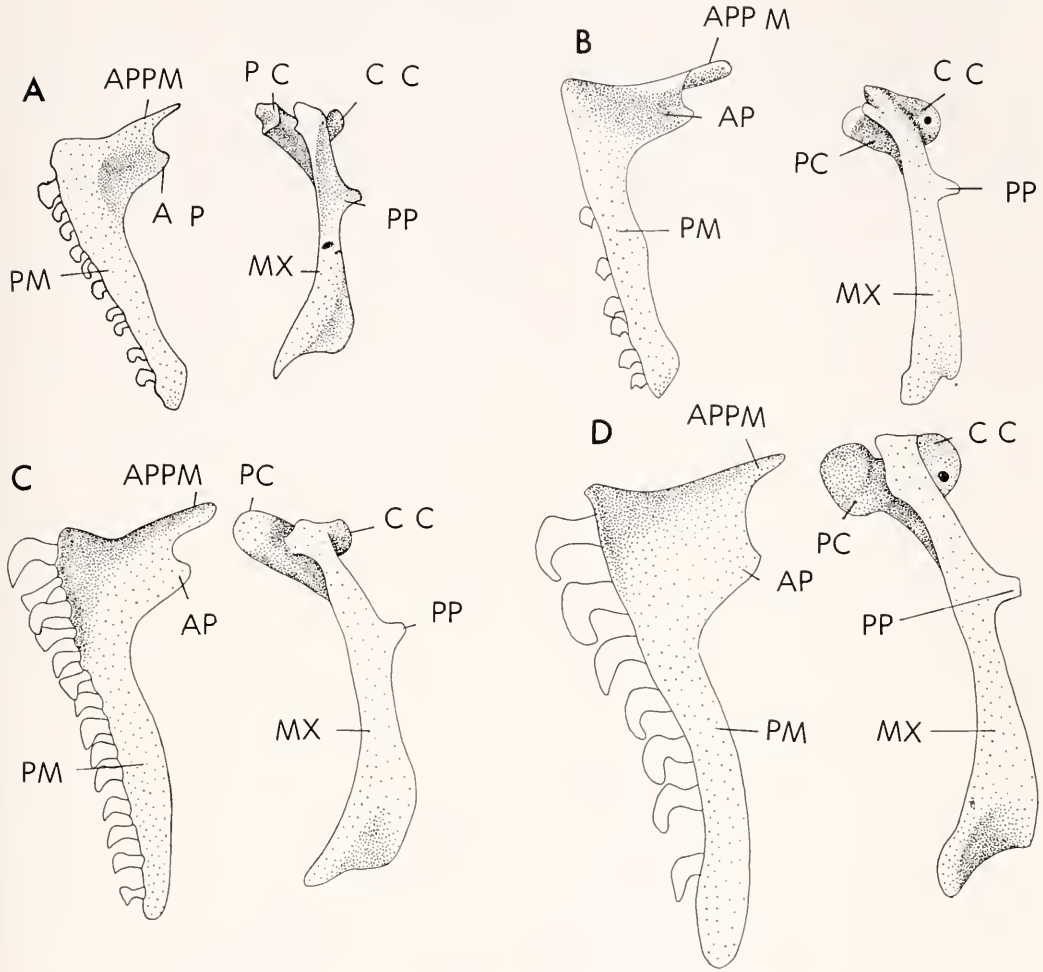


Figure 7. Lateral aspect of upper jaws. A, *eccentricus*; B, *microlepis*; C, *hecqui*; D, *paradoxus*.

maintained in a monotypic genus because of presumed planktivorous feeding habits (Poll, 1956, p. 413) and its dentition composed of obtusely pointed and posteriorly recurved small teeth arranged in a single row numbering 22–45 on the upper jaw and 19–40 on the lower jaw. However, our studies on stomach contents have revealed that *X. hecqui* feeds predominantly on scales of cichlids. We are therefore including *X. hecqui* into the lepidophagous trophic category.

Perissodus Boulenger 1898 represents a monotypic genus; it is characterized by broad-based truncated teeth arranged in a single row numbering 18–26 and 16–18 respectively on the upper and lower jaws.

Plecodus Boulenger 1898 with four species (*paradoxus, elaviae, straeleni,* and *multidentatus*) has laminar, strongly recurved or curled teeth. In the type species, *paradoxus,* the teeth are arranged in a single row numbering 18–20 and 12–15 respectively on the upper and lower jaws.

Neurocranium

The skull roof is broad both interorbitally and across the otic region in all lepidophagous species. Characteristic features of this lepidophagous skull type are the relatively decurved dorsal profile giving the orbital margin a rounded circumference, a rather high cranial vault and the relatively short ethmovomerine region. All these neurocranial features correspond with those of the generalized *Haplochromis bloyeti* as described by Greenwood (1974) and *H. burtoni.* However, all lepidophagous neurocrania deviate from the generalized form in three specializations: (1) The parasphenoid, at the level of the posterior orbit, slopes forwards and upwards when viewed laterally (Figs. 2, 3:PS). Such an abrupt angling of the parasphenoid gives the lepidophagous neurocranium a very unique lateral profile, not generally encountered in other trophic groups; (2) The preorbital region is shorter, with a more vertically oriented prefrontal-lateral ethmoid complex; (3) well-differentiated apophyses, representing attachment sites for the palatine, are present on the lateral aspect of the ethmoid (Figs. 2, 3:PF, LE, E) and the lateral flange of the lateral ethmoid-prefrontal.

Interspecific differences are mostly confined to the preorbital region. The floor of the rostral fossa in the cranial roof is formed by anteromedial shelves of the frontals in *paradoxus, straeleni, elaviae,* and *multidentatus* (Fig. 4B), whereas in *hecqui, microlepis* and *eccentricus* the ethmoid is also involved in the composition of the floor of the rostral fossa (Fig. 4:A, C, E). Concomitantly the lateral ethmoid-prefrontal complex is more vertical in *paradoxus, elaviae, straeleni* and *multidentatus* (Figs. 2, 3:PF, LE) than in *hecqui, microlepis* and *eccentricus.* The supraoccipital crest is relatively low and does not extend farther anteriorly than midway between the orbits (Figs. 2, 3:SOC), except in *straeleni* in which the high occipital crest reaches the posterior rim of the rostral fossa.

Suspensory Apparatus

All lepidophagous species share the following specializations in the suspensory apparatus (Figs. 5, 6): (1) strong, sutural connections between the following pairs of bones, the symplectic process of the hyomandibular-metapterygoid, the metapterygoid-entopterygoid, and the palatine-ectopterygoid; (2) the vertical and horizontal limbs of the preoperculum are at a 90 degree or nearly 90 degree angle to each other and enclose a prominent adductor fossa; (3) the large palatine has large vomerine and prefrontal processes.

Only a few interspecific differences have been found in the suspensory apparatus. The palatine in *hecqui* (Fig. 6A:P) is more slender than in other species, although it has well-differentiated prefrontal and vomerine processes. Vertically oriented ectopterygoids are found in *microlepis, eccentricus* and *straeleni* whereas in *paradoxus, multidentatus* and *hecqui* the bones are slightly oblique (Figs. 5, 6:ECT).

Jaw Apparatus

A unique specialization of the maxilla shared by all lepidophagous cichlids of Lake Tanganyika is a prominent process originating from the posterior margin of the maxilla (Figs. 5, 7:MX, PP). This blunt but slender posterior maxillary process is directed caudally. Neither muscle nor special ligamentous attachments are associated with this process which is located within the connective tissue which extends between the upper jaw and the cheek. The function of the posterior maxillary process is unknown.

All lepidophagous species also share the following specializations: (1) The proximal tip of the maxillary body is blunt and abbreviated (Figs. 5, 6, 7:MX); (2) Ventrally the maxilla possesses an extra flange for attaching the enlarged maxillomandibular ligament; (3) The premaxillae have short ascending processes and prominent articular processes (Figs. 5C, 7:APPM, AP); (4) The dentary is the dominant element in

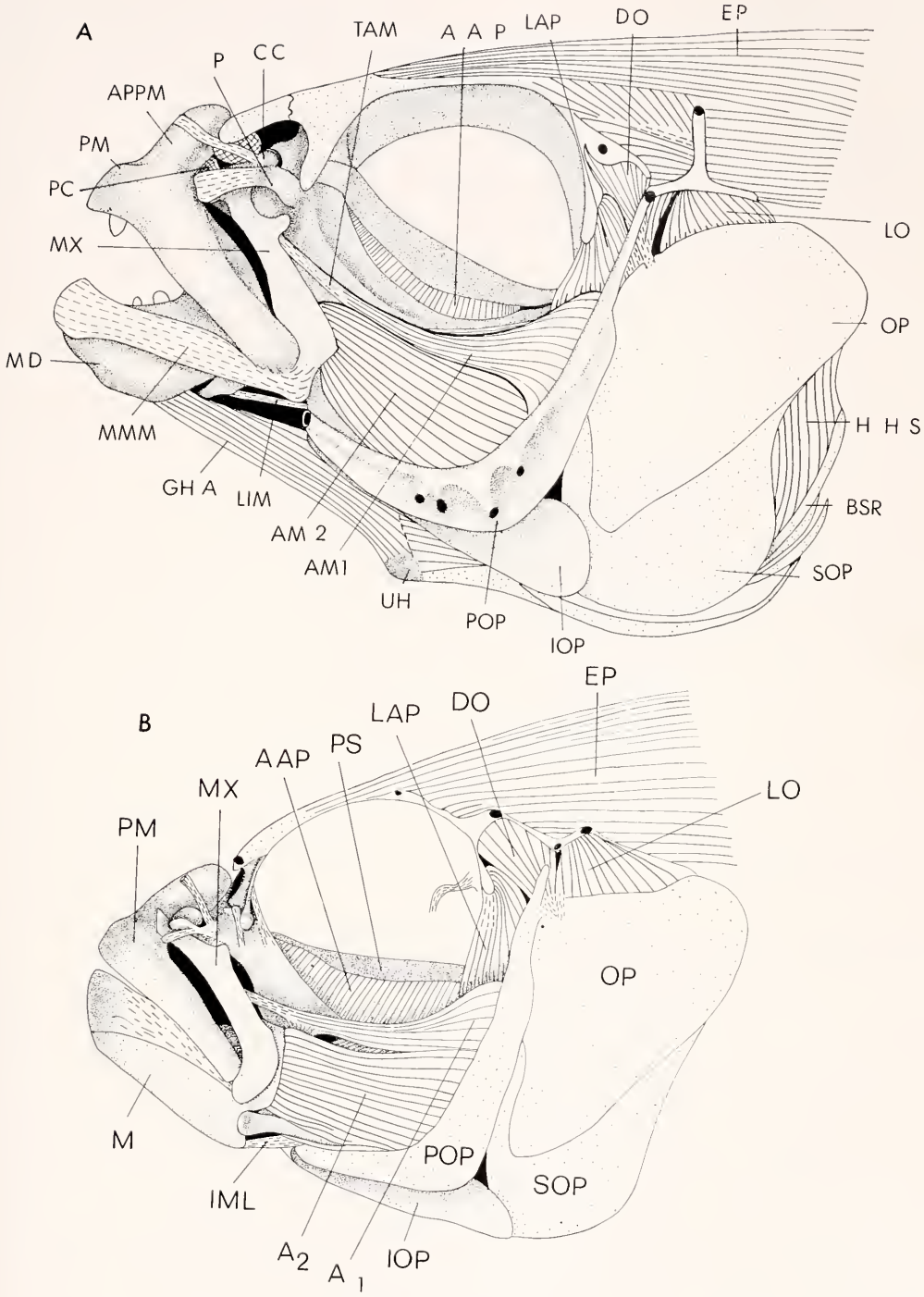


Figure 8. Lateral aspect of cephalic muscles after removal of lacrimal, circumorbital bones and eyeball. A, *eccentricus*; B, *hecqui*.

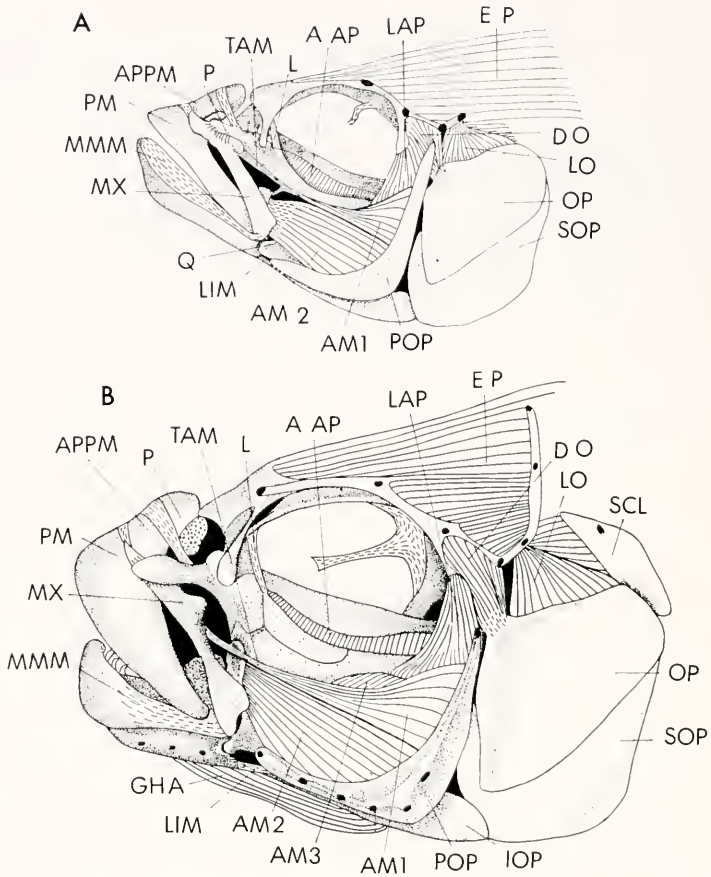


Figure 9. Lateral aspect of cephalic muscles after removal of lacrimal, circumorbital bones and eyeball. A, *microlepis*; B, *paradoxus*.

the mandible; the small anguloarticular is excluded from the dorsal margin, although it possesses a high ascending process (Figs. 5, 6:A, D).

Interspecific differences of the maxilla are especially discernable in the shape of the maxillary body. A strongly concave profile of the anterior margin of the maxilla is found in *hecqui, paradoxus,* and *eccentricus,* whereas in *microlepis* and *multidentatus* it is only slightly concave. Relatively long mandibles characterize *hecqui* and *multidentatus,* while *eccentricus, microlepis* and *paradoxus* possess shorter and deeper mandibles (Figs. 5, 6, 7:MX).

Intrinsic Ligaments of the Jaw Apparatus

All lepidophagous cichlids of Lake Tanganyika possess a very thick and broad ligament within the lower lip, extending from the anterior tip of the dentary to the ventral tips of the premaxilla and maxilla (Figs. 8, 9:MMM). Histologically, it appears as a prominent tract of collaginous fibers. This ligament may help stabilize the jaws especially when the mouth is opened widely during the bite. Concomitantly the maxillomandibulare mediale and anterius ligaments are hypertrophied. No interspecific differences have been found.

Adductor Mandibulae Muscles

The intramandibular division of the adductor complex is divided into two distinct units in all lepidophagous cichlids of Lake Tanganyika (Fig. 10B:IAM_1:IAM_2). The dorsal head represents the original intramandibularis (adductor mandibulae pars A_w) retaining the typical topography, while the larger ventral head originates tendinously from the medial aspect of the quadrate at the quadratomandibular joint level and inserts on the medial surface of the mandible (Fig. 10B:IAM_2). Such a distinct subdivision also occurs in algae-scraping cichlids from Lake Tanganyika and Malawi, suggesting a role in closing the strongly abducted lower jaw.

Adductor Arcus Palatini

With the exception of *hecqui*, the lepidophagous cichlids are characterized by a reduction in relative fiber length of the adductor arcus palatini (Figs. 8, 9:AAP) and by the shelflike dorsal extension of the entopterygoid and metapterygoid. This extension narrows the distance between the parasphenoid and the dorsal rim of the suspensory apparatus. In *hecqui* (Fig. 8B: AAP), the adductor arcus palatini resembles that of more generalized cichlids (Goedel, 1974a, b; Liem and Osse, 1975).

Dorsal Branchial Muscles

All lepidophagous cichlids of Lake Tanganyika have a hypertrophied anterior levator internus (Fig. 13:LI) functioning as the antagonist of the retractor dorsalis (RP).

Other specializations shared by *microlepis*, *eccentricus*, *paradoxus*, *straeleni* and *elaviae* include: (1) Drastic reduction of all transversus dorsalis muscles. The transversus dorsalis anterior, originally composed of three separate heads, loses the second head which runs from the anterior surface of the second pharyngobranchial to partially blend into the longitudinal musculature of the esophagus while the

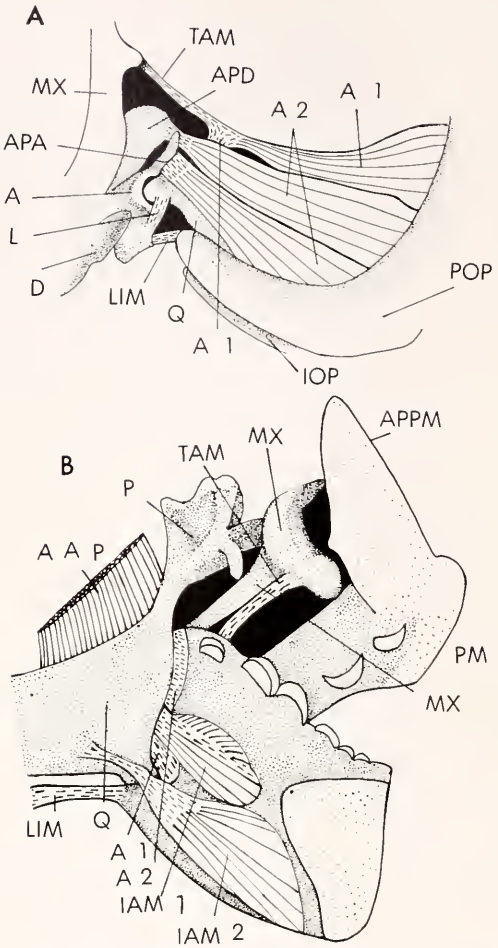


Figure 10. A, lateral view of adductor mandibulae muscles and surrounding bones in *eccentricus*; B, medial aspect of upper and lower jaws and associated muscles in *paradoxus*.

other fibers insert on the medial surface of the third and fourth pharyngobranchials. The third head (transversus obliquus) runs from the anterior surface of the second epibranchial to an aponeurosis from its fellow of the other side although there is always a small part with an aponeurotic attachment to the parasphenoid. Anteriorly the first head, which runs between the anterior surfaces of the pharyngobranchials, is retained in all lepidophagous cichlids, although it is greatly reduced in *eccentri-*

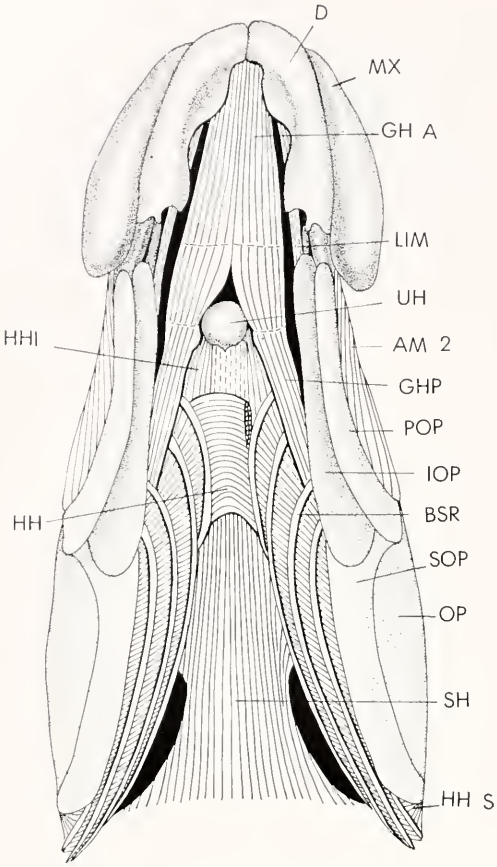


Figure 11. Ventral aspect of muscles of the head of *eccentricus*.

cus (Fig.13:TDA, TDP); (2) The weakly developed transversus dorsalis posterior runs without interruptions between the tubercles on the dorsal aspects of the toothplates of the fourth branchial arch; (3) Another marked reduction affects the obliquus posterior which runs between the muscular process of the lower pharyngeal jaw (= fifth ceratobranchials) and the posteromedial face of the fourth epibranchial (Fig. 13:OF).

In *hecqui* and *multidentatus* the dorsal branchial musculature resembles that of the usual cichlid type, e.g., *Tilapia* (Goedel, 1974a, b). The three heads of the transversus dorsalis anterior (Fig. 13B, D:TDA) are clearly differentiated and the obliquus posterior is not atrophied.

Ventral Branchial Musculature

Two muscles in this region play a dominant role in all lepidophagous cichlids of Lake Tanganyika. The rectus communis (pharyngohyoideus) is hypertrophied and possesses two bellies separated by either a tendon or tendinous inscription. Concomitantly its functional antagonist, the pharyngocleithralis internus, (Liem, 1973), (pharyngoclavicularis internus) is also hypertrophied (Fig. 12A, B:PHH, PCI).

DISCUSSION

Generic Revision

The generic identities of *Perissodus*, *Plecodus* and *Xenochromis* as originally envisioned by Boulenger (1898, 1899) were based on tooth morphology, and the number of teeth, dorsal spines and gill rakers. The genera were defined as follows:

Perissodus Boulenger 1898 (p. 21), type (and only) species *microlepis*, by original designation, has broad-based, enlarged, truncated teeth with the formula $\frac{18-26}{16-18}$, 18–21 gill rakers and 17–19 dorsal fin spines.

Plecodus Boulenger 1898 (p. 22), type species *paradoxus* by original designation, has large laminar and inwardly curled teeth with the formula $\frac{18-20}{12-15}$, 20–23 gill rakers and 18–20 dorsal fin spines. This genus has four species.

Xenochromis Boulenger 1899, type (and only) species *hecqui* by original designation, has compressed recurved teeth with the formula $\frac{22-45}{19-40}$, 47–57 gill rakers and 16–17 dorsal spines.

With the discovery of *Plecodus multidentatus* by Poll (1952) the morphological and meristic gap between *Plecodus* and *Xenochromis* was bridged because *multidentatus* possesses relatively small recurved teeth with slender cylindrical bases (Plate 2, Fig. 29), 23–26 gill rakers, 16–17 dorsal spines and the dental formula $\frac{33-40}{30-35}$. The jaw dentition of the newly discovered spe-

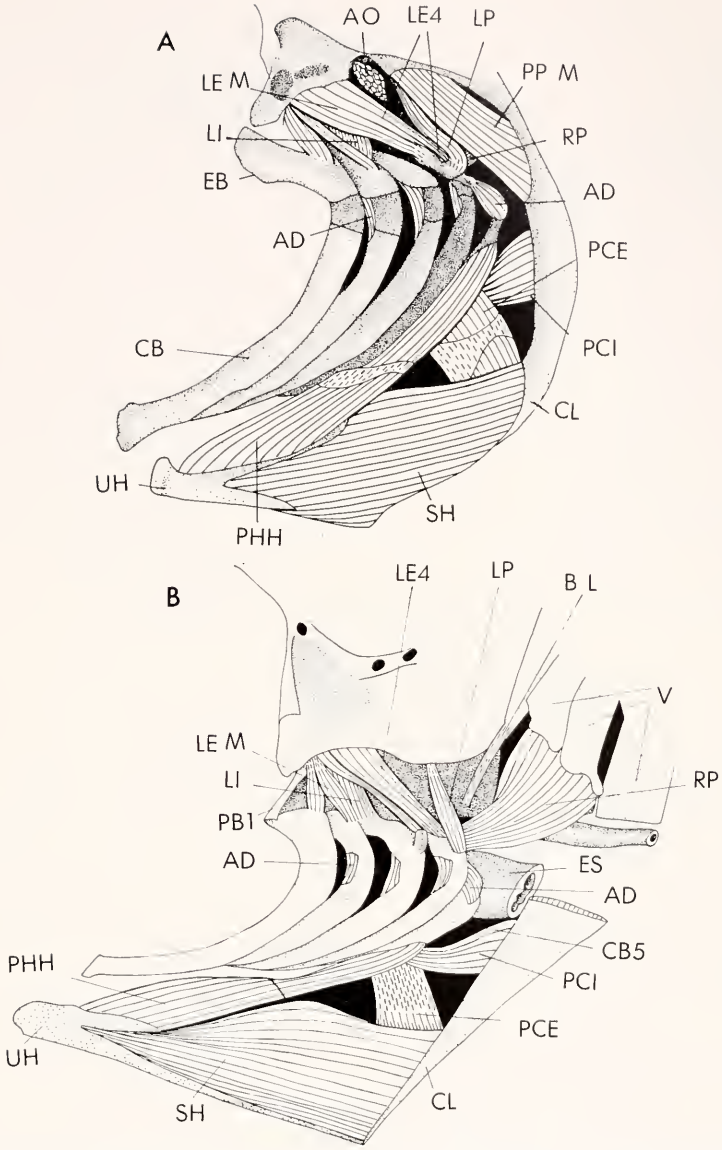
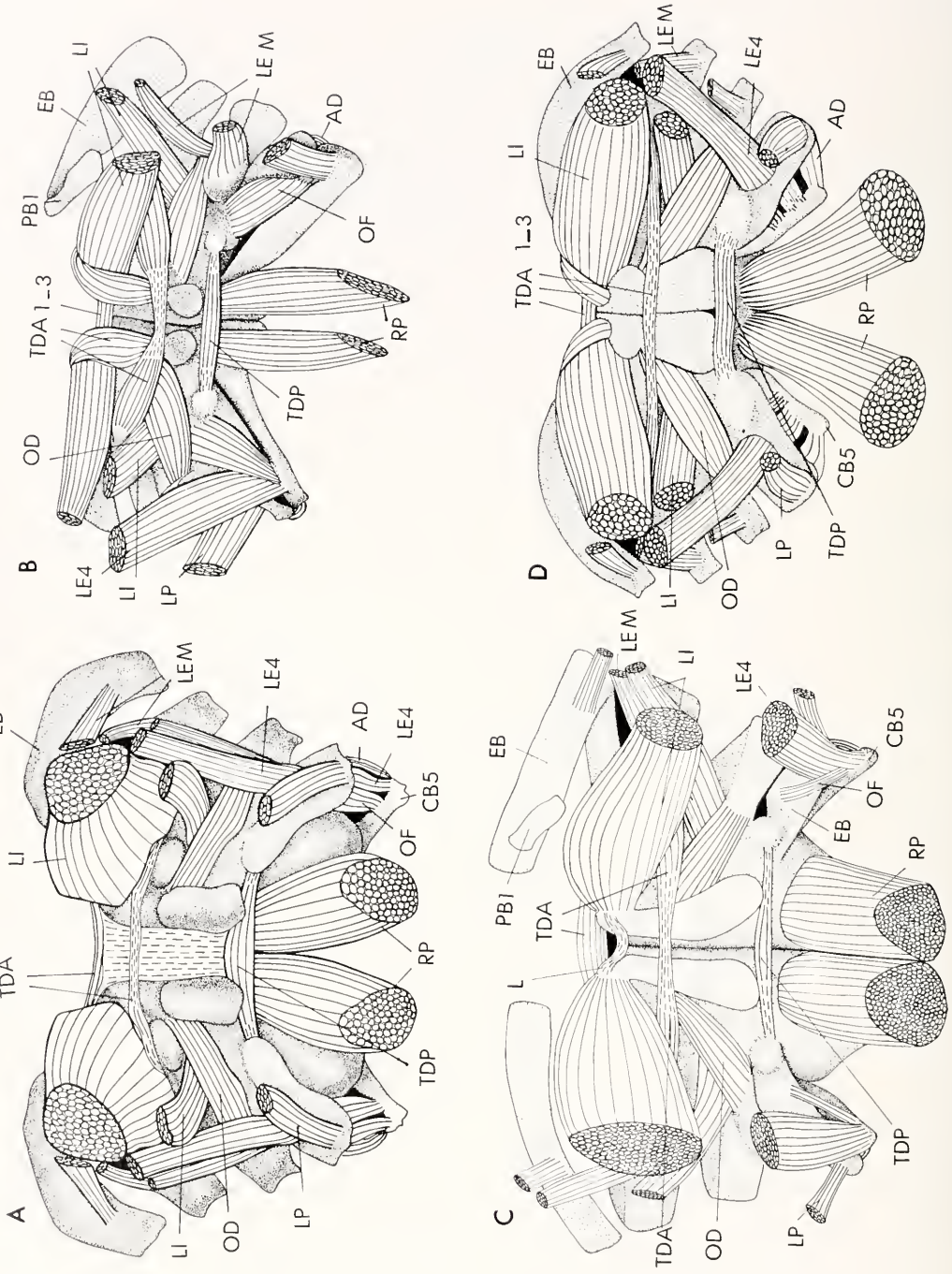


Figure 12. Lateral view of branchial apparatus and muscles after removal of operculum, suspensory apparatus, gills, gill rakers and mucous membrane. A, *eccentricus*; B, *microlepis*.

cies, *eccentricus*, bridges the gap between *Perissodus* and *Plecodus* especially since in a juvenile *eccentricus* the anterior mandibular teeth are broad-based with obtuse tips, whereas the lateral premaxillary teeth are strongly recurved (Plate 2; Figs. 25, 26, 28).

We have shown that the anatomy of the lepidophagous cichlids of Lake Tanganyika presents an unusual picture of a virtually complete morphological intergradation between the generalized (i.e., *hecqui*) and the specialized (i.e., *eccentricus*).

Now the question is whether all the con-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stituent species of this gradal complex (i.e., *hecqui, multidentatus, paradoxus, straeleni, elaviae, microlepis* and *eccentricus*) represent a truly monophyletic lineage or whether we are dealing with a web of parallelisms.

Our study of all known species comprising the lepidophagous cichlids of Lake Tanganyika has resulted in the discovery of the following unique combination of salient specializations shared by all members of the group: (1) The variously expanded jaw teeth arranged in a single row are either remarkably recurved, broadened, coiled or obtusely pointed in a truly unique fashion which doubtless facilitates the removal of scales from other fishes (Plates 1, 2; Figs. 23–31). Similarly-specialized tooth shapes have not been encountered in any other known cichlid; (2) The elongate maxilla possesses a posterior maxillary process, not shared with any other known cichlid of Lake Tanganyika (Figs. 5, 7:PP); (3) The parasphenoid exhibits an abrupt dorsal curvature at the level of the posterior orbit giving the neurocranium of this group a characteristic lateral profile (Figs. 2, 3:PS); (4) In the dorsal branchial musculature, the anterior levator internus muscle is dominant both structurally and functionally, a feature not shared by other cichlids of Lake Tanganyika (Fig. 13:LI); (5) An exceptionally thick ligament within the lower lip runs between the anterior tip of the dentary and the distal ends of the maxilla and premaxilla (Figs. 8, 9:MMM); (6) In the mandible the dentary is greatly enlarged, excluding the articular from the dorsal margin (Figs. 5, 6:D, this specialization is shared with algae-scraping cichlids of Lake Tanganyika ([Liem and Osse, 1975]); (7) The palatine has evolved additional processes to strengthen the palato-neurocranial connection. Similar conditions are found in algae-scraping cichlids, e.g., *Eretmodus, Spathodus* and *Tanganicodus;* (8) The intramandibularis (A_w) muscle is divided into two separate units. The ventral, and largest, of these originates from the quadrate and inserts on the ventromedial aspect of the mandible. (Fig. 10B: IAM_1, IAM_2).

It is clear that this combination of eight specialized characters link all lepidophagous species of Lake Tanganyika into a monophyletic lineage. Because of this basic homogeneity in specialized morphology we exclude the possibility that several unrelated species are ancestors. Within this assemblage we can recognize two primitive and five derived species (see next section). On the evidence presented above, we include all the species of this monophyletic lineage in one genus. Since *Perissodus* Boulenger 1898 (p. 21) with the type species *microlepis*, has priority over *Plecodus* Boulenger 1898 (p. 22) and *Xenochromis* Boulenger 1899, the monophyletic lepidophagous lineage composed of *hecqui, multidentatus, paradoxus, elaviae, straeleni, microlepis* and *eccentricus* is classified within the genus *Perissodus*, which is defined by the above mentioned combination of specialized characters.

Interrelationships of *Perissodus* species

As the base line of this study we have identified as generalized those characters shared by *Haplochromis burtoni*, an insectivorous species with a riverine distribution but also occurring in Lake Tanganyika. Many of the myological features in *H. burtoni* resemble those of *Tilapia* as described by Goedel (1974a, b). Having established the morphological nature of a generalized species in Lake Tanganyika, we hope to determine the evolutionary directions of the various species of *Perissodus*.

←

Figure 13. Dorsal view of dissected and isolated branchial apparatus and muscles. A, *eccentricus*; B, *hecqui*; C, *microlepis*; D, *multidentatus*.

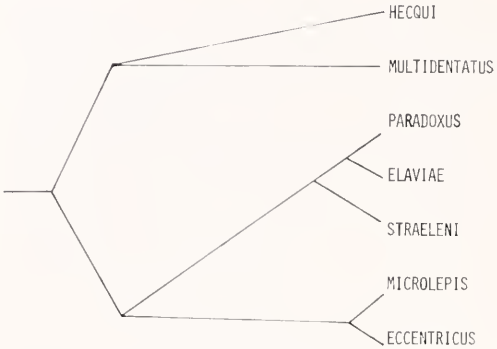

Figure 14. Proposed phyletic relationships within the genus *Perissodus*.

The greatest number of primitive characters has been found in *P. hecqui* and *P. multidentatus*. Both species retain (a) the generalized pattern of the three heads of the transversus dorsalis anterior muscle, (b) the well-developed obliquus posterior (Figs. 13B, D:TDA, OF), (c) a higher number of jaw teeth than other related species, (d) the elongate mandible, and (e) the rounded shape of the articular apophyses on the dorsal surfaces of the third pharyngobranchials (Fig. 13B, D). *P. hecqui* appears to be the most primitive representative of this lineage since it is the only species with a relatively unspecialized palatine, an unmodified adductor arcus palatini, and a preopercular with a shallow and relatively restricted adductor fossa. Although *P. hecqui* and *P. multidentatus* differ from each other in respect to dentition, number of gill rakers in the lower part of the first arch, and the distal configuration of the mandible, the two taxa can be regarded as sister species since they share the character of an increased number of gill rakers in the lower part of the first gill arch (Fig. 14).

In all other, more specialized species, the second head of the transversus dorsalis anterior is lost, the obliquus posterior becomes atrophied, and the mandible is shortened and deepened (Figs. 13, 5, 6). The articular apophyses on the dorsal surface of the third pharyngobranchial becomes elongate (Fig. 13A, C), the anterior levator internus is hypertrophied (Fig. 13:LI), and the greatly enlarged jaw teeth are either curled inwardly or become truncated or obtusely pointed (Plates 1, 2: Figs. 23–31).

We can recognize a clear dichotomy in the five specialized species. In one lineage comprised of the sister species *P. microlepis* and *P. eccentricus* (Fig. 14) tooth specialization involves a broadening of the tooth base while distally the tooth form becomes truncated or obtusely pointed. Both species usually have at least some premaxillary teeth recurved as in other *Perissodus* but never laminar as in the next species group. This second lineage, represented by *P. elaviae*, *P. paradoxus*, and *P. straeleni* (Fig. 14), exhibits such salient specializations as strongly curled laminar teeth and the loss of the third head of the transversus dorsalis anterior muscle. *P. straeleni* deviates from the sister species pair, *P. paradoxus-elaviae* in respect to the high supraoccipital crest extending anteriorly to the posterior rim of the rostral fossa.

Functional Analysis of Lepidophagous Mechanism

Stomach contents have established that all species of *Perissodus* except *hecqui* feed on fish scales (Marlier and Leleup, 1954; Poll, 1956). Our observations indicate that *P. hecqui* feeds predominantly on scales, although some individuals do eat copepods and insect larvae. The scales are definitely from percoid fishes and some have been identified as cichlid caudal fin scales. Some long, deep, ctenoid scales are almost certainly body scales of cichlids. We have not encountered clupeid or centropomid scales in the stomachs of *P. hecqui*. One species, *P. straeleni*, has been studied in an aquarium where it fed exclusively on scales (Fryer and Iles, 1972, p. 89). These fish remove scales by opening the jaws as widely as possible and pressing the mouth against the prey. Subsequent strong adduction of the jaws leaves a denuded spot

on the prey's body. From these observations we assume that *Perissodus* removes scales by biting rather than by rasping small scales from the two sides of the caudal fin, a method used by *Corematodus* in Lake Malawi and *Haplochromis welcommei* in Lake Victoria.

The functional prerequisites for collecting scales by a biting mechanism are a powerful and stable adductor system and a capability to open the mouth widely and variedly so that the upper and lower jaws can be pressed intimately against the surface of the body of the prey.

Extreme abduction of the mandible is made possible by relatively deep articulatory surfaces of the anguloarticular, permitting the mandible to rotate around the quadratomandibular joint in a wider angle (Greenwood, 1967). In the upper jaw, the ascending processes of the premaxillae are greatly shortened (Figs. 7, 8, 9:APPM). Short ascending processes of the premaxillae free the premaxilla from constraints on rotation around a transverse axis. The distal tip of the alveolar process of the maxilla can then be rotated anteroventrally over a much longer distance to occupy a nearly vertical position, matching a similar position of the fully abducted mandible. Apart from the deeper articulatory configuration of the quadratomandibular joint and the shortened ascending processes of the premaxillae, no other specializations can be correlated with the ability to open the jaws widely. The jaw opening mechanisms depend on the action of three couplings as discussed by Liem (1970), and Liem and Osse (1975).

The abducted jaws are stabilized by the hypertrophied collaginous tract within the lower lip (Figs. 8, 9:MMM), and strongly developed medial and anterior maxillomandibular ligaments. The strongly abducted mandible creates some mechanical problems for the adductor system. During the wide-open phase of the mouth the insertion site of pars A_2 of the adductor mandibulae muscle is close to the quadratomandibular joint, resulting in a drastically diminished moment arm. Contraction of the adductor mandibulae pars A_2 muscle will therefore be very ineffective in closing the widely opened jaws. The hypertrophied second head of the intramandibularis muscle (Fig 10A, B), on the other hand, can change the direction of the working line of the pars A_2 of the adductor mandibulae muscle. The adaptive significance of the enlarged and separate new division of the intramandibularis muscle lies in its ability to create a favorable working line for the adductor mandibulae muscle when it pulls up the fully abducted mandible.

In most *Perissodus* it can be inferred from stomach contents that scales have been manipulated and arranged on top of each other to form discrete packets. The pharyngeal jaw apparatus (composed of the firmly united and toothed fifth ceratobranchials, the upper toothplates of the second, third and fourth branchial arches, and the muscles associated with all of these [see Liem, 1973]) may manipulate the scales to form manageable packets prior to deglutition. Special adaptations of the pharyngeal jaw apparatus have evolved to enhance this process. Within the lepidophagous lineage we can detect a distinct trend towards: (a) elongate articular surfaces of the basipharyngeal joint (Liem, 1973) which enhance longitudinal movements (Fig. 13:A, C); (b) the loss of one or two heads of the transversus dorsalis, drastic reduction of the remaining head(s) and the transversus dorsalis posterior muscle (Fig. 13); (c) hypertrophied anterior levator internus, retractor dorsalis, rectus communis and pharyngocleithralis internus muscles (Figs. 12, 13).

Greater control and mobility of the upper pharyngeal jaw is the most important specialization correlated with superior scale manipulating capabilities. Based on electromyographical evidence we can conclude that the retractor dorsalis (Liem, 1973) and the anterior levator internus (Liem, in preparation) are antagonistic muscles,

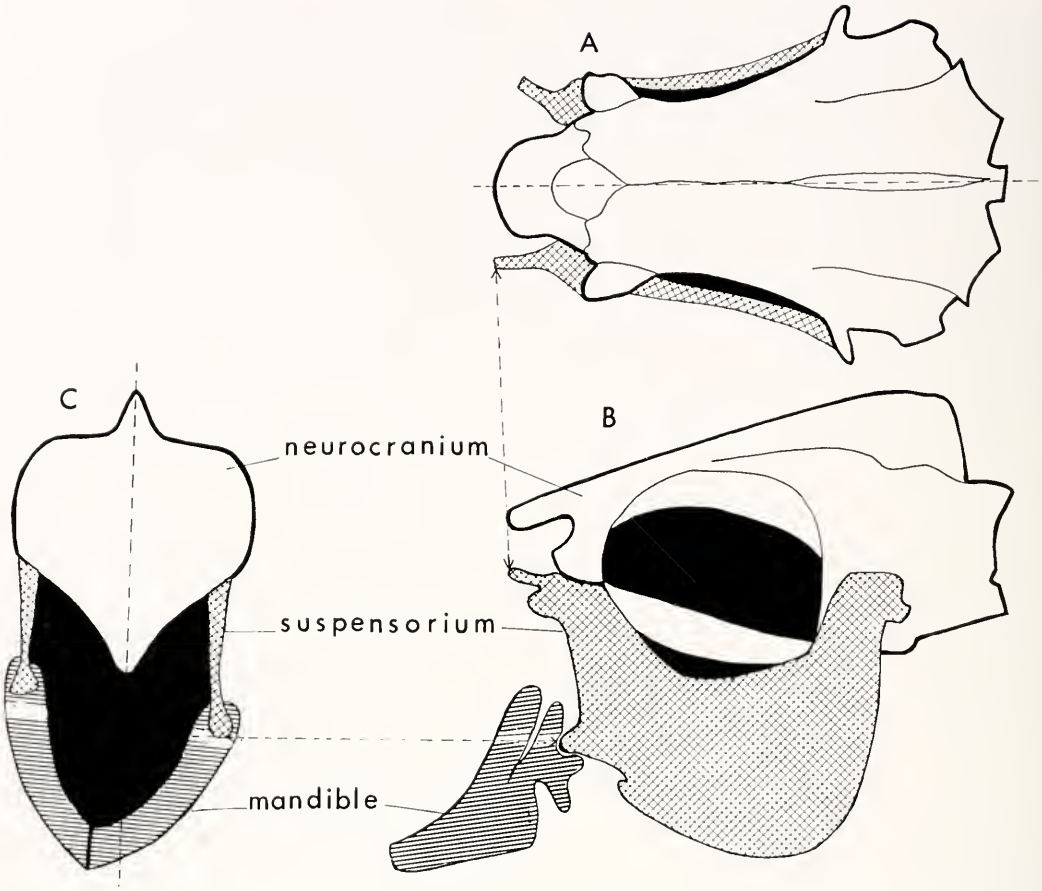

Figure 15. Diagrammatic representation of asymmetry in *eccentricus*. A, dorsal view of neurocranium, suspensory apparatus and mandible; B, lateral view of neurocranium, suspensory apparatus and mandible; C, frontal view of neurocranium and suspensory apparatus.

which, in conjunction with the elongate articular surfaces of the pharyngeal jaws, can produce controlled and more extensive protraction, retraction and adduction of the upper pharyngeal jaws. Because the upper pharyngeal jaws of either side can be controlled independently (Liem, in preparation), the additional specializations give the lepidophagous pharyngeal jaw apparatus the necessary controlled mobility to manipulate scales into packets. Morphological reduction of all constrictors seem to indicate that movements produced by long-fibered muscles are selected for, while movements produced by shorter fibered ones play a much diminished role. The lower pharyngeal jaw apparatus does not deviate much from the pattern characterizing all cichlids. However, more extensive movements, in coordination with those of the upper pharyngeal jaws, are realized by the hypertrophied and elongated rectus communis and pharyngocleithralis internus muscles (Fig. 12). Coordinated actions of the fourth levator externus, pharyngocleithralis internus and the rectus communis with its posterior attachment on the fifth ceratobranchial (Fig. 12:LE_4, PCI, PHH) enable the upper and lower pharyngeal jaws to remain in close or near

apposition for long periods during the manipulatory cycle. Meanwhile, the anterior levator internus and retractor dorsalis cause the controlled longitudinal and rocking movements around the elongate basipharyngeal joint. Within the lepidophagous lineage, *P. hecqui* and *P. multidentatus* have a rounded and small articular apophysis of the basipharyngeal joint (Fig. 13B, D), suggesting that they may have only limited abilities to arrange scales in packets. Stomach contents of *P. hecqui* do not reveal scales in packets, but more studies are required to verify this preliminary observation.

Functional Significance and Evolutionary Origin of Jaw Asymmetry

Asymmetry of the jaw apparatus of *P. eccentricus* is unique among the large order Perciformes. When the mouth is opened, the upper and lower jaws deviate either to the left or to the right side respectively in sinistral and dextral individuals (represented in equal numbers in our population sample [Plate 1: Figs. 17, 18, 19, 20, 22]). As asymmetry of jaw opening and protrusion is accompanied by asymmetrically arranged teeth (Plate 1: Figs. 20, 22), a given individual can bite scales from just one side of its prey depending on direction of approach (i.e., front or back). Asymmetrical jaws may provide *P. eccentricus* with a mechanism by which it can approach its prey much more stealthily than its symmetrical counterparts; it should be able to strike very effectively while its body is parallel to that of its prey. If prey can only be approached from behind, a sinistral *P. eccentricus* could only strike them on the right side. It would therefore be understandable that sinistral and dextral individuals occur in the same frequencies as such a distribution makes the best use of food resources.

It was noted that a few preserved *P. elaviae* also had jaws projecting slightly to one side when open but none had noticeably asymmetrical teeth. *P. elaviae* appears

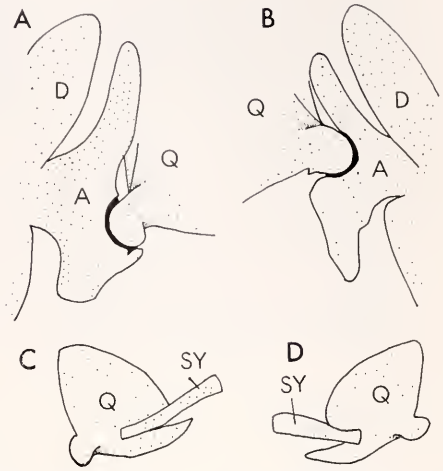

Figure 16. Lateral view of quadratomandibular region in *eccentricus*. (A, left; B, right) and symplectic-quadrate complex (C, left; D, right). (Dextral specimen.)

to be a deep-water counterpart of *P. paradoxus* in the same way that *P. eccentricus* is distributed deeper than its sister species, *P. microlepis*, although the depth distributions of *P. elaviae* and *P. paradoxus* overlap somewhat.

Functionally, the asymmetrical opening of the jaws uses the following mechanism. In a dextral individual, the right mandible can be dropped farther ventrally than the left one because the deeper articulatory socket of the right articular (Fig. 16) gives the right mandible a wider abduction angle (Greenwood, 1967, p. 53). In dextral individuals the distance between the quadratomandibular joint and the place where the interoperculum attaches to the suboperculum is larger on the right side than on the left. Consequently, the "kinematic efficiency" is higher on the right side. (Kinematic efficiency is defined by Anker [1974] as the ratio of the distance between the operculomandibular joint and the attachment of interopercular to operculum on one hand, and quadratomandibular joint and the attachment of interoperculum to operculum on the other hand.) In dextral individuals, a higher kinematic efficiency on the right side means that a *smaller*

PLATE 1

Fig. 17. Lateral view of dextral *P. eccentricus*.

Fig. 18. Lateral X-ray photograph of same specimen as Figure 17.

Fig. 19. Frontal view of same specimen as Figure 17.

Fig. 20. Ventral view of upper jaw of *P. eccentricus*.

Fig. 21. Scanning electron micrograph of lateral aspect of lateral premaxillary teeth of *P. eccentricus*.

Fig. 22. Dorsal view of lower jaw of *P. eccentricus*.

Fig. 23. Scanning electron micrograph of anterodorsal aspect of anterior mandibular teeth of *P. paradoxus*.

Fig. 24. Scanning electron micrograph of dorsal aspect of mandibular teeth of *P. hecqui*.

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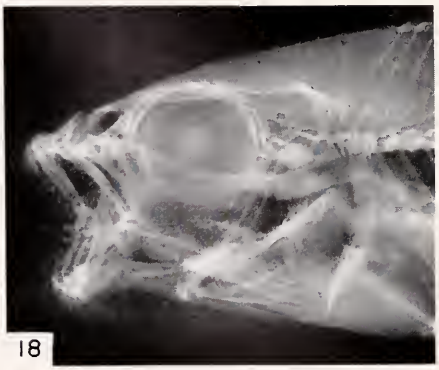

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PLATE 2

Fig. 25. Scanning electron micrograph of ventrolateral aspect of anterior premaxillary teeth of *P. eccentricus.*

Fig. 26. Scanning electron micrograph of lateral aspect of second anterior premaxillary tooth of *P. eccentricus.*

Fig. 27. Scanning electron micrograph of lateral aspect of anterior mandibular teeth of *P. hecqui.*

Fig. 28. Scanning electron micrograph of lateral aspect of lateral premaxillary tooth of *P. eccentricus.*

Fig. 29. Scanning electron micrograph of anterodorsal aspect of mandibular teeth of *P. multidentatus.*

Fig. 30. Scanning electron micrograph of dorsolateral aspect of premaxillary teeth of *P. microlepis.*

Fig. 31. Scanning electron micrograph of posterior aspect of anterior mandibular teeth of *P. hecqui.*

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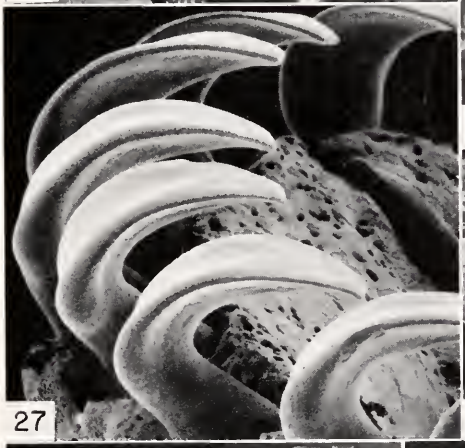
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rotation angle for the right interopercular-subopercular and opercular series can achieve a *larger* rotation angle for the right half of the mandible. The superimposition of a deeper quadratomandibular joint upon the higher kinematic efficiency on a given side will result in a pronounced asymmetrical movement of the mandible. Since the upper jaw is morphologically and functionally coupled to the mandible (Liem, 1970), the asymmetrical movement of the latter will be automatically translated to the former. A special adaptive feature allowing for a highly efficient asymmetrical movement of the upper jaw is the asymmetrical suspension of the maxillae from the maxillary processes of the palatines (Fig. 15A, B). In a dextral individual, the maxillary process of the right palatine is turned more laterally than the left (Fig. 15A), thus re-enforcing the asymmetrical forces transmitted from the mandible. The resulting mechanism assures a perfectly asymmetrical coordination of upper and lower jaws.

The morphological basis of this complex asymmetrical jaw apparatus is surprisingly simple. A configural change in the articulatory surface of the jaw-joint on one side has far reaching functional consequences leading to pronounced asymmetrical patterns in jaw movements. This functional asymmetry has been re-enforced by bilateral differences in the kinematic efficiency of the levator operculi-opercular apparatus-mandible coupling which opens the jaws. These efficiency differences result from a topographical shift of the quadratomandibular joint on one side (Fig. 15C). Asymmetrical differences in the relative position of the quadratomandibular joints are correlated with just two structural elements within the suspensory apparatus, i.e., in dextral individuals the left symplectic is longer and more oblique compared with the right one (Fig. 16). From the evidence presented by *P. eccentricus*, we may conclude that the asymmetrical position of the quadratomandibular joint is determined by growth centers associated with the symplectic-quadrate complex. Such a simple ontogenetic cause supports the hypothesis that the underlying morphological principle in the evolution of the trophically complex and morphologically varied lacustrine cichlids is differential growth in various skull-elements (Greenwood, 1973, 1974; Liem, 1973; Liem and Osse, 1975). Since such salient differences can evolve by bilateral asymmetry in one individual, we may conclude that the discovery of this new species supplies further indirect evidence that simple genetic alterations can slightly affect the scheduling or velocity of ontogenetic events, which in turn are capable of producing adult phenotypic changes of rather profound dimensions.

SUMMARY

Scale-eating in lacustrine cichlid fishes is one of the most extraordinary trophic specializations evolved during the explosive phase of cichlid adaptive radiation, which resulted in optimal partitioning of all food resources. Within this distinctive scale-eating lineage, characterized by unique adaptations, we have recorded a sustained and prevailing evolutionary trend towards occupation of progressively narrower adaptive zones. A new, asymmetrical form seems to represent the summit of the scale-eating trend. Pronounced asymmetry of the jaw mechanism may have been selected for as a mechanism enabling the scale-eater to approach its prey in a strategically favorable fashion. The morphogenetic mechanisms underlying this asymmetry are bilateral differences in differential growth rates of two bones in the jaw suspension and the remodeling of articular surfaces of the lower jaw joints. It is postulated that such mechanisms are controlled by relatively simple genetic factors governing the velocity or timing of ontogenetic events. Asymmetry has furnished the flatfishes (Pleuronectiformes) with a most effective mechanism to exploit the benthic habitats in an extremely efficient way. The capacity of cichlids to evolve asymmetry of the jaw

mechanism rapidly by simple morphogenetic alterations represents another example that fewer adaptive compromises are necessary if more parameters controlling form can vary independently. However, the potential to evolve asymmetry of jaws to optimize trophic functions rapidly has not been realized in other cichlids, indicating that asymmetrical jaws possess only a limited selective value in lacustrine habitats. It is possible that the process of specialization has reached its summit in this new species (which may be at the end of an evolutionary blind alley), although we must be aware of the subjectivity of our judgment of specialization, and the limitations of our imagination.

Key to Species of *Perissodus* Boulenger 1898

1. S.L./depth 3.0–4.35; less than 9 scales between lateral line and dorsal fin origin ... 2
– S.L./depth 2.5–2.95; 10–11 scales between lateral line and dorsal fin origin; max. size 160 mm ..... *P. straeleni* (Poll) 1948.
2. Teeth small, contiguous, all about equal size, 18–40 on mandible 3
– Teeth large, spaced, of unequal sizes, 12–23 on mandible 4
3. Mandible broadly rounded; 47–57 gill-rakers on lower part of first arch; lateral line 57–65; max. size 280 mm ..... *P. hecqui* (Boulenger) 1899.
– Mandible narrow, pointed; 23–26 gill-rakers on lower part of first arch; lateral line 69–73; max. size 139 mm ..... *P. multidentatus* (Poll) 1952.
4. Anterior mandibular teeth laminar strongly curled inward 5
– Anterior mandibular teeth truncated or obtusely pointed, not laminar or curled inward 6
5. Upper and lower jaw teeth 18–20/12–15; A.III, 12–13; lateral line 68–78; S.L./depth 3.75–4.15; max size 290 mm ..... *P. paradoxus* (Boulenger) 1898.
– Upper and lower jaw teeth 22–37/18–23; A.III, 10–11; lateral line 64–67; S.L./depth 3.0–3.8; max. size 320 mm ..... *P. elaviae* (Poll) 1949.
6. Lateral mandibular teeth bilaterally symmetrical; 17–18 dorsal spines; upper and lower lateral lines 45–51/22–32; max. size 111 mm ..... *P. microlepis* Boulenger 1898.
– Lateral mandibular teeth asymmetrical; 14–15 dorsal spines; upper and lower lateral lines 51–60/32–45; max. size 128 mm ..... *P. eccentricus* n. sp.

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The Orb-weaver Genera *Verrucosa*, *Acanthepeira*, *Wagneriana*, *Acacesia*, *Wixia*, *Scoloderus* and *Alpaida* North of Mexico (Araneae: Araneidae)

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THE ORB-WEAVER GENERA *VERRUCOSA*, *ACANTHEPEIRA*, *WAGNERIANA*, *ACACESIA*, *WIXIA*, *SCOLODERUS* AND *ALPAIDA* NORTH OF MEXICO (ARANEAE: ARANEIDAE)

HERBERT W. LEVI[1]

ABSTRACT. North of Mexico are found one species each of *Verrucosa*, *Wagneriana*, *Acacesia*, *Scoloderus* and *Alpaida*, four species of *Acanthepeira*, of which two are new, and three of *Wixia*, of which one is new. Most species of these genera, except *Acanthepeira*, are tropical American; the Nearctic species are found in the eastern half of the United States, except that *Wixia globosa* is found in the Southwest. Morphological intermediates of the *Acanthepeira* species are found. Among these genera, diversity of habits and web structure is much greater than would be expected from studies based on groups with mainly temperate distributions.

INTRODUCTION

Most orb-weavers are tropical and information about the few well-known north temperate orb-weavers has been generalized erroneously. Lack of information on tropical species has permitted arachnologists to study web structure only superficially, and there is as much diversity in habits and behavior as there is in web structure. The tropical orb-weavers tantalize with their promise of exciting behavioral adaptations to be discovered once we know the species.

Not only do orb-webs differ in structure, but, more importantly, they differ in when and how they are used. Most species do not share the well-known habits of *Araneus diadematus* (Witt, *et al.*, 1968): making a web early in the morning just before daylight, keeping the orb up a day, tearing down all but the frame lines during the night. *Araneus* species are generally nocturnal, but leave their webs up during the day. *Acacesia hamata* makes its fine-meshed, previously unknown, web at dusk, and hauls it in at daybreak, only to make a new web in a different place the following evening (Plate 5). *Verrucosa arenata* makes a large, loose web low in trees each morning or evening and removes it after sunrise; this species rests head up in its web (Plates 1, 2), the reverse of the usual orb-weaver resting position. The *Scoloderus* web is a long ribbon (Plate 6) with the hub at one end. As it has only recently been found, we may suppose it is a nocturnal web. Other orb-weavers in the tropics pull their webs in only a few hours after completing them (W. Eberhard, personal communication). In Panama I observed a large *Eriophora* sp. female, closely related to the group treated here, making a huge web, about 60 cm diameter, after dark every night. By morning the web had disappeared, and a new one was made the following evening after dark. Not even frame threads were left during the day and the spider itself disappeared. While *Verrucosa arenata* makes a flimsy retreat on a leaf (Plate 1), *Acacesia hamata* makes no retreat at all but depends on its coloration to make it disappear among foliage (Plate 5). *Wixia* is believed to make its web high in trees, and the spider probably rests

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Plate 1. *Verrucosa arenata*. Above: web. Below: female in retreat and two males sparring. (Photographs by A. Moreton and J. Carico.)

Plate 2. *Verrucosa arenata* in web facing up. (Photograph by A. Moreton.)

tightly appressed to a twig rather than in a silky retreat.

Aside from the observations reported here, almost nothing is known about feeding habits. An old observation recently republished (Forster and Forster, 1973) that *Celaenia* catches only male moths suggests the use of pheromones to attract prey.

While noctural orb-weaving spiders are brown in color with disruptive patterns that make them difficult to find during daytime (Plate 5), diurnal orb-weavers, which hang during the day in the middle of the web, are brightly colored, often silvery (*Argiope, Leucauge, Tetragnatha, Nephila*). Perhaps the silver reflects light and heat, or makes them hard to see in meadows among plants (*Argiope*, Levi, 1969). Other diurnal orb-weavers have spines on the abdomen (*Gasteracantha, Micrathena*), perhaps obscuring their outlines. The white zigzag stabilimentum, which appears only in the webs of diurnal orb-weavers, is the subject of a controversy regarding its origin and function. While many orb-weavers take their webs down in pouring rain, *Cyrtophora* and perhaps also *Mecynogea* keep theirs up. Although their webs are inefficient for catching insects, and energy-consuming to construct, they alone take advantage of the insect abundance following a tropical downpour (Y. Lubin, 1973, 1974).

Sometimes it is surprisingly easy to sort spider specimens into populations that represent species by using a combination of morphological characters, but, as this study progressed, difficulties presented themselves. In *Acanthepeira*, some specimens do not fit, and the species appear to hybridize. The species differ not only in the structure of the epigynum but also in the shape of the abdomen, the size, and the armature of the fourth coxa and leg in males. I can only make students of spiders aware of this species problem to which laboratory study yields no solution. Only field work in the southeastern states can resolve the problem of the various intermediates between *Acanthepeira* species.

The species included in this paper all are related to *Eriophora* (Levi, 1970), and, more distantly, to *Araneus* (Levi, 1971, 1973). All are Nearctic representatives of tropical American genera, except that members of *Acanthepeira*, though related to the tropical orb-weavers described here, are found north of Mexico.

I would like to thank W. G. Eberhard, J. E. Carico and his students, and A. Moreton for making observations and photographs available. Particularly, Jim Carico provided unique observations and photographs. Specimens for this study were made available by J. A. Beatty; D. Bixler; J. E. Carico; C. Dondale, Canadian National Collections; H. Dybas and J. B. Kethley, Field Museum; W. J. Gertsch; D. C. Lowrie; B. J. Kaston; A. Moreton; W. W.

Plate 3. *Acanthepeira stellata* in web. Above: female. Below: juvenile male. (Photographs by A. Moreton.)

Plate 4. *Acanthepeira venusta* female.

Moss and D. G. Rentz, Academy of Natural Sciences of Philadelphia; R. Matthews; W. B. Peck; N. I. Platnick, American Museum of Natural History and Cornell University Collections; S. Riechert; V. D. Roth; R. Schick, California Academy of Sciences; W. Sedgwick; K. J. Stone; H. K. Wallace; F. R. Wanless, British Museum, Natural History; H. V. Weems, Florida State Collection of Arthropods. The study and its publication were supported in part by the National Sciences Foundation grant GB–36161. L. R. Levi reconstructed my faltering syntax.

Verrucosa McCook

Verrucosa McCook, 1888, Proc. Acad. Natur. Sci. Philadelphia, p. 78. Type species *Epeira arenata* Walckenaer (= *E. verrucosa* Hentz) by tautonymy and monotypy [*Verucosa* original misspelling]. The name is feminine.

Mahadiva Keyserling, in O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 53.

Mahadeva Marx, 1890, Proc. U. S. Natl. Mus., 12: 541. Type species *Epeira verrucosa* Hentz by monotypy.

Note. O. P.-Cambridge and also Marx attribute the name to Keyserling, 1892, Spinnen Amerikas, 4: 67. In Keyserling *Mahadeva* is spelled with an e.

Diagnosis. *Verrucosa* females differ from those of other genera by having the abdomen as wide as long, or wider than long, with tubercles at the posterior end and a dorsal, white, glossy mark (Fig. 1). Males differ from those of other genera by having, on the second left tibia, a branch bearing two short macrosetae (Fig. 7). The palpus differs from that of male *Parawixia* in having the paramedian apophysis fused to the proximal end of the long conductor (Fig. 9). The females, unlike those of other Araneidae, rest in the web head up (Plate 2).

Genitalia. The base of the epigynum bears an annulate scape, very long in *V. arenata* (Fig. 3), in *V. undecimvariolata* the length equal to the width of the base. In *Verrucosa* alone among related genera, a pair of lateral lamellae enclose the base of the epigynum, small in *V. arenata* (Fig. 4), very large in *V. undecimvariolata.*

In the palpus of *Verrucosa* males alone, the paramedian apophysis is fused to the proximal end of the long, narrow conductor, giving a hint as to the origin of this sclerite found in the palpi of only these related genera. The base of the embolus, called the stipes when a separate sclerite, has distal hematodocha and bears a terminal apophysis with a long distal spine (Figs. 9, 10). The embolus has a lamella, narrow, pointed, and running parallel to it in *V. arenata* (Figs. 8, 11), wide in *V. undecimvariolata.* In addition, the embolus of *V. undecimvariolata* has a mitten-shaped shield toward the mesal side. The median apophysis in both species is long and narrow, parallel to the narrow conductor, and has a hook-shaped basal extension opposed to the paramedian apophysis.

Coloration. The carapace, sternum, and coxae are light to dark brown with paired darker gray patches on carapace. Legs brown and banded, with proximal ends of some articles lighter. Dorsum of the female abdomen blackish with a white triangle pointing posteriorly (Fig. 1). Venter of abdomen black in *V. arenata* with paired

Plate 5. *Acacesia hamata*. Top: female in web. Left: female on vegetation. Right: web. (Top and right photographs by J. Carico.)

white spots (Fig. 2), or with a central white spot in *V. undecimvariolata*. The male abdomen has only indistinct marks (Fig. 6).

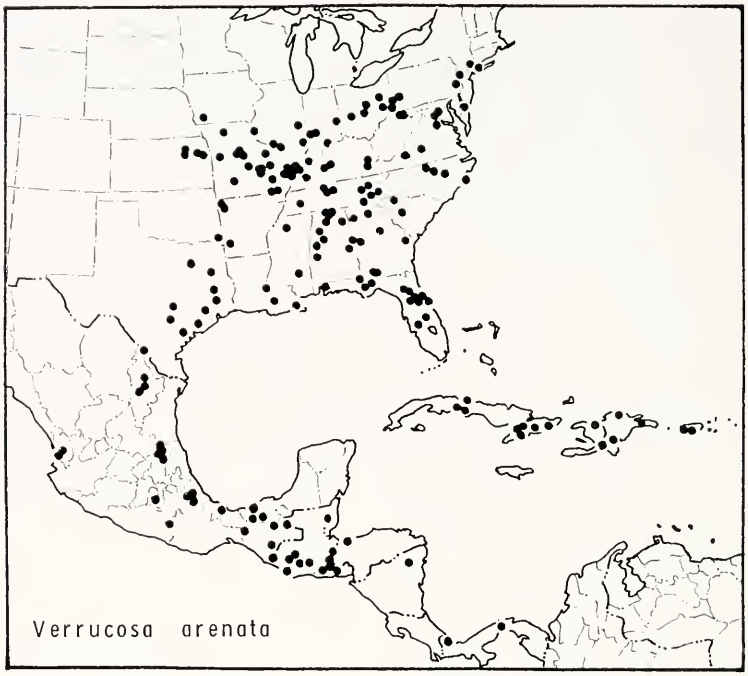
Structure. The eye area of the female is wide in front, the laterals far from medians (Fig. 1). The height of the clypeus equals the diameter of the anterior median eyes.

The swollen head area is delimited anteriorly by a shallow groove between the posterior median and posterior lateral eyes, and posteriorly by a deeper diagonal groove toward the thoracic area (Fig. 1). There are dark patches in the grooves and no thoracic depression in the female. The male carapace is narrower in the eye region, lacks the grooves between median and lateral eyes and has a shallow thoracic depression traversed by a longitudinal line (Fig. 6). The anterior median eyes are the largest, the laterals smallest. The anterior median eyes are slightly more than their diameter apart and the posterior medians about their diameter apart. The female abdomen is somewhat sclerotized, subtriangular, wide in front, pointed behind with lateral humps and tubercles along the posterior and sides (Fig. 1). The abdomen of the smaller male is longer than wide, with indistinct lateral and posterior tubercles, and some dark, dorsal sclerotized disks (Fig. 6). The palpal femur has a basal tooth facing that of the endite. The palpal patella has only one seta. The first coxa has a hook fitting into a depression of the second femur, and the swollen second tibia has a long spur bearing two macrosetae, and a shorter spur bearing one (Fig. 7). The males have relatively longer legs than the females. The first, second and fourth femora of the males have a single row of macrosetae on the venter, the first and second femora of the females a double row, and the tarsi lack large setae in both sexes.

Species. Verrucosa are all American. Only one species, *V. arenata*, occurs north of Mexico, and its range extends into Central America (Map 1). In southern Mexico and Central America the sympatric *V. undecimvariolata* is smaller in size, has a wider abdomen, a central, ventral white spot, and differs in details of the genitalia. A third species is *V. meridionalis* (Keyser-

←

Plate 6. *Scoloderus tuberculifer* web. (Photograph taken in Colombia by W. Eberhard.)



Map 1. Distribution of *Verrucosa arenata* (Walckenaer).

ling) of southern Brazil, with a relatively narrow abdomen, and the scape of the epigynum wider than that of *V. undecimvariolata*.

Misplaced species.

Epeira alticeps Keyserling, 1879 is an *Alpaida*. NEW COMBINATION.

Epeira audax Blackwall, 1863, belongs to *Paraneixia*. It is found in Brazil. Specimens of the Marx collection were mislabeled as coming from North America.

Verrucosa rubronigra Mello-Leitão, 1939 is a juvenile *Alpaida*. NEW COMBINATION. The female has recently been redescribed under the name *Acrosoma riscoi* Archer, 1971. NEW SYNONYMY.

Verrucosa arenata (Walckenaer)
Map 1, Figures 1–11, Plates 1, 2

Epeira mexicana Lucas, 1833, Mag. Zool. Guérin, classe 8, pt. 1, pl. 3, ♀. Female specimens from Mexico and Guatemala, lost. NEW SYNONYMY, NOMEN OBLITUM.

Epeira arenata Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 133, ♀. Female syntypes, Abbot manuscript illustration p. 16, fig. 165, p. 17, figs. 181–183, ♀; male, p. 29, fig. 360, from Georgia in the British Museum, Natural History. Copy in the Museum of Comparative Zoology, examined.

Epeira verrucosa Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 19, pl. 3, fig. 2, ♀. Female syntypes from North Carolina and Alabama in the Boston Society of Natural History, destroyed. Emerton, 1902, Common Spiders, p. 181, figs. 421–423, ♀, ♂.

Verrucosa arenata, – McCook, 1888, Proc. Acad. Nat. Sci., Philadelphia, p. 78. 1893, American Spiders 3: 200, pl. 12, figs. 6, 7, ♀, ♂. F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 482, pl. 45, figs. 23, 24, ♀, ♂. Comstock, 1912, Spider Book, p. 465, fig. 480, ♀. Petrunkevitch, 1930, Trans. Connecticut Acad. Sci., 30: 329, figs. 211, 212. Comstock, 1940, Spider Book, rev. ed., p. 479, fig. 480, ♀. Roewer, 1942, Katalog der Araneae, 1: 879. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 229, figs. 735–736, ♀. Bonnet, 1959, Bibliographia Araneorum, 2(5): 4789.

Mahadiva reticulata O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 54, pl. 3, fig. 10, ♂. Male type from Volcan de Chiriquí, Panama in the British Museum, Natural History, not examined. Keyserling, 1892, Spinnen Amerikas, 4: 71, pl. 3, fig. 55, ♂.

Figures 1–11. *Verrucosa arenata* (Walckenaer). 1. Female, dorsal. 2. Female, venter of abdomen. 3–5. Epigynum. 3. Ventral. 4. Posterior. 5. Posterior, cleared. 6. Male, dorsal. 7. Second tibia of male, anterior view. 8–11. Left palpus. 8. Mesal view. 9. Expanded, subventral. 10. Expanded, subdorsal view. 11. Embolus and conductor.

Abbreviations. a, terminal apophysis; c, conductor; dh, distal hematodocha; e, embolus; h, basal hematodocha; m, median apophysis; pm, paramedian apophysis; r, radix; t, tegulum; y, cymbium.

Scale lines. 0.1 mm, except Figs. 1, 2, 6, 1.0 mm.

Mahadeva [sic] *verrucosa*, – Keyserling, 1892, Spinnen Amerikas, 4: 72, pl. 3, fig. 56, ♀, ♂.

Araneus aequiangulus Franganillo, 1930, Inst. Nac. Invest. Cienc. Habana, 1: 70, fig. 9, ♀. Female type in the Cuban Academy of Science, Havana in unlabeled vials. Franganillo, 1936, Aracnidos de Cuba, p. 69. NEW SYNONYMY.

Araneus aequiangulus, var. *ochraceus* Franganillo,

1930, Inst. Nac. Invest. Cienc. Habana, 1: 72. Female type in the Cuban Academy of Science, Havana in unlabeled vials. Franganillo, 1936, Araenidos de Cuba, p. 70. NEW SYNONYMY.

Note. The illustration and description of Lucas' leave little doubt that his *Epeira mexicana* is an older name for this common species. As the name *arenata* has been used many more than ten times during the last 100 years, I consider *mexicana* a nomen oblitum. Furthermore, the name *Verrucosa mexicana* has been used for the Central American *Verrucosa undecimvariolata*, an erroneous nineteenth century synonymy of Simon.

Description of female from Tennessee. The abdomen has no setae but some sclerotized spots on sides. Total length, 8 mm. Carapace 3.5 mm long, 3.0 wide. First femur, 4.9 mm; patella and tibia, 5.0; metatarsus, 3.6; tarsus, 1.3. Second patella and tibia, 4.0 mm; third, 2.2; fourth, 3.5.

Male. Total length, 5.5 mm. Carapace 2.5 mm long, 2.2 wide. First femur, 4.5 mm; patella and tibia, 4.7; metatarsus, 4.0; tarsus, 1.1. Second patella and tibia, 2.9 mm; third, 1.6; fourth, 2.2.

Variation. Verrucosa females may be yellow or white. Females north of Mexico vary from 5.0 to 9.5 mm total length, carapace 2.3 to 3.7 long, 2.2 to 3.5 wide. Males north of Mexico vary from 4.0 to 6.1 mm total length, carapace 2.2 to 3.0 long, 1.9 to 2.5 wide. Individuals from each collection are about the same size, the smallest specimens coming from the Gulf states, the largest from southern Mexico and Central America, where the species competes with the smaller *V. undecimvariolata*. A female from the Panama Canal Zone measured 11.9 mm total length, carapace 5.2 long, 4.2 wide.

Diagnosis. Females have the scape reaching almost to the spinnerets and there is a small white spot on each side of the scape in the black area (Fig. 2). In the Central American *V. undecimvariolata* the venter has a large central white spot and a very short scape, covering less than half the distance from epigynum to spinnerets. In the male of *V. arenata* the palpal embolus tapers evenly to the tip (Figs. 8, 11); that of *V. undecimvariolata* has an upper lobe, and the subterminal apophysis (?) near the base of the embolus is more sclerotized.

Natural History. Males are mature in August and September in the northern part of their range, females from early August to October. This species is commonly found in woods, but also in gardens. The female makes a retreat in a broad leaf, usually on the upper side, by bending the leaf along its long axis and fastening it with strands of silk (Plate 1). The retreat is made on a low, overhanging branch of a tree that faces an open area such as a yard or field. The vertical web is triangular with the upper strand slightly off the horizontal to 45°. The retreat is always at the highest point of the web. Spirals range from 20 to 32 complete turns, average about 25. There are about 19–22 radii. Area of web incorporating the spirals measures about 60 × 90 cm (Plate 1). The web is usually made in the early morning, from midnight until about 3:00 h, and is removed shortly after sunrise. This timing varies widely, and is often disrupted by weather conditions such as rain, strong winds, etc. Webs are not made every morning, especially with older females (unpublished observations of ten females near Lynchburg, Virginia by Robert McMichael, Glen Rubis and J. E. Carico). Ms. A. Moreton (in letter) reported that a female near Powhaton, Virginia built a web in the early evening between 19:00 and 22:00 h and took the web down between 9:00 and 10:00 h in the morning. One male was found about 4 cm from the retreat of the female. Another male crawled up the upper foundation thread toward the retreat, periodically giving a series of 4 to 5 jerks on the thread. The female, resting in the hub during this time, responded each time with 4 to 5 jerks. When the second male reached the vicinity of the retreat, the males exchanged jerks, approached each other, and combat oc-

curred (by this time, the female had moved to her retreat), resulting in eviction of the first male (Plate 1). The second male began wandering soon thereafter, fed upon some of the coarser parts of a lower foundation thread, and left the vicinity. This observation was made at approximately 7:30 h, 14 September 1974. The female removed her web at 9:10 h (Robert McMichael, Glen Rubis, and J. E. Carico, in letter). The female rests in the web with the head up (Plate 2).

Distribution. Eastern states, from southern New York state to Iowa and northeastern Kansas, south to Panama; West Indies (Map 1).

Acanthepeira Marx

Acanthepeira Marx, 1883, in Howard, List of Invertebrates of South Carolina, p. 22. Type species designated by Bonnet, 1955, Bibliographia Araneorum, 2: 125, is *Acanthepeira spinosa*, a nomen nudum (thus unavailable as type species). I here designate *Epeira stellata* Walckenaer the type of the genus. The generic name is feminine.

Marxia McCook, 1893, American Spiders, 3: 192. Type species by original designation *Epeira stellata* Walckenaer. The generic name is feminine.

Note. Marx, in his list of South Carolina spiders, listed three specific names in combination with *Acanthepeira,* one of them *stellata*, but did not indicate that the name *Acanthepeira* was new. The name thus was not used until Kaston (1938) substituted it for *Marxia*. Since then it has been the only generic name in use for *A. stellata.* Because the name *Acanthepeira* first appeared in Marx's list without comment, the name has not even been listed in the *Zoological Record* or by Neave (1939).

Diagnosis. Acanthepeira has the anterior eye row procurved as seen from in front, the lateral eyes closer to the clypeus than to the medians; the height of the clypeus in the median area is about two to three diameters of the anterior median eyes. The lateral eye tubercle differs from *Wagneriana* and all other genera in being spine-shaped, pointing anteriorly (Figs. 12, 13). As in *Wagneriana,* the head part of the carapace appears swollen and is much higher than the eye area immediately in front of it (Fig. 13). The abdomen has a projecting anterior median tubercle (Fig. 12); there is no such hump in the related *Parawixia* and *Wagneriana.*

Genitalia. The scape of the female epigynum is a short compact drawn-out cone bent posteriorly, differing in shape in different species. The short scape is not set off from the base (Figs. 14, 29, 36, 51).

The palpus, especially the embolus, appears to be relatively simple. There are no apophyses or lamellae attached to the embolus (Fig. 21). As in other genera described here, and less so in the related *Eriophora* (Levi, 1970), the attachment of the bulb differs from that of *Araneus* species as all sclerites face the median, and are completely hidden by the tegulum in lateral view (Figs. 19, 20). In *Araniella, Nuctenea, Zygiella, Araneus, Neoscona, Singa, Hypsosinga, Larinia,* and *Mangora* the terminal apophysis is distal and crowns the palpal bulb, while in *Singa* the terminal apophysis covers even the lateral side. There is no terminal apophysis in *Acanthepeira* and in the related *Eriophora,* but there is a paramedian apophysis (pm in Fig. 21) on which the base of the embolus (e) rests. The paramedian apophysis is hidden in the contracted embolus by the cymbium (y). There is no scale or cap on the embolus and adult males are found from spring until fall. Males appear to be longer lived than those of *Araneus,* which can mate only once. The palpal patella has one macroseta, as is characteristic of this group of genera. The first coxa of the male lacks the distal hook present in *Parawixia* and *Wagneriana.*

Coloration. Carapace has white setae and a narrow light border around dark sides of thorax, and black rings around posterior median eyes. Chelicerae brown. Sternum brown, indistinctly marked. Legs with narrow bands. Abdomen brown with

Map 2. Distribution of *Acanthepeira* species. Open circles are records of specimens which appear intermediate.

indistinct light and dark marks on dorsum, and dark spots on venter, but white marks are lacking except sometimes in *A. venusta*, which may have a white transverse mark or two white spots side by side behind the genital groove.

Structure. Carapace highest in head region, lacking a thoracic depression in female, but with a shallow indistinct depression in male. In size, the anterior median eyes are slightly larger or subequal to secondary eyes; in females of *A. stellata* the anterior medians are smaller. The anterior median eyes are about their diameter apart, the posterior medians 1.2 to 1.5 diameters apart in females, one to two diameters in males. The anterior margins of the chelicerae each have one tooth at the base of the fang and three or four at some distance; the posterior margin has four teeth and denticles. The abdomen is soft and the number of tubercles varies within species, but there is always an anterior median tubercle. In some specimens

of *A. marion*, the caps of the tubercles are slightly sclerotized (Fig. 40). The abdomen of *A. venusta* is narrower and the anterior median tubercle longer than in other species (Fig. 55).

Species. The species look similar. They differ in size, but sizes overlap. Females differ in the structure of the scape, males in the armature of the last coxa and femur (Figs. 22–28), but only slightly in the palpi (Figs. 19, 35, 41, 56). Males also differ slightly in leg length, but this character overlaps. The first patella-tibia of *A. cherokee* is 1.1 times carapace length, of *A. marion* 1.1 to 1.3, of *A. stellata* 1.2 to 1.3, and of *A. venusta* 1.3 to 1.4.

As far as I know, there are no *Acanthepeira* species other than the four species from North America.

Species problems. It is exceedingly difficult to separate some *Acanthepeira* specimens from the southeastern United States and it appears that three species interbreed. Specimens that appear to be intermediates have been found (Figs. 45–50, note difference in size).

Perhaps there were originally three species in the Southeast: *A. cherokee*, most distinct in structure and habitat preference (moist bottomland woods); the large *A. marion*; and the small, common *A. venusta*. Then, with the spread of the intermediate-sized *A. stellata* into Florida, perhaps species barriers broke down, and introgression occurred between *A. marion*, *A. stellata*, and *A. venusta*. In most theridiid and araneid species, the Florida specimens are the smallest. However, Florida specimens of *A. stellata* are larger than those from other parts of the range, possibly as a result of competition with the small *A. venusta*. Only field work in the southeastern states can answer some of the questions.

Misplaced species. Two species have been incorrectly assigned to this genus. The types of both are lost in the United States National Museum. Judging by the illustrations, neither has the anterior median tubercle characteristic of *Acanthepeira*.

Marxia grisea McCook, 1893, American Spiders, 3: 195, pl. 13, fig. 10, ♀. Female type allegedly from "Biscayne Bay, Florida," an erroneous Marx locality. Specimen lost in the Marx collection of U. S. National Museum. The size of *M. grisea* as described by McCook is much smaller than that of *A. marion*, although the epigynum may be similar. This species is probably a South American *Parawixia*, perhaps a *Wagneriana*.

Epeira moesta Keyserling, 1892, Spinnen Amerikas, 4: 108, pl. 5, fig. 80, ♀. Female type is allegedly from "Mariposas, Arizona," an erroneous Marx locality. Specimen lost in the Marx collection of the U. S. National Museum. This species is probably a South American *Wagneriana*, perhaps *Parawixia*.

Key to *Acanthepeira* Species, Females

1. Scape of epigynum longer than width of epigynum at base (Figs. 36, 51). 2
– Scape of epigynum as long or shorter than width of epigynum at base (Figs. 14, 29). 3

2(1) Total length 6 to 10 mm; abdomen narrow, length 1.5 times its width, with anterior median tubercle pointed and projecting (Fig. 55); epigynum 1.6 mm long, scape flattened (Fig. 51); Virginia to Alabama, common in Florida, Cuba. ..... *venusta*
– Total length 10 to 16 mm; abdomen about as long as wide, median anterior tubercle not projecting above carapace (Fig. 40); epigynum more than 2 mm long, scape round in cross-section (Fig. 36); Pennsylvania, Missouri, Tamaulipas to Florida. ..... *marion*

3(1) Epigynum with a constriction proximal to swollen basal portion of scape (Fig. 29); Maryland, Missouri, Texas to Florida. ..... *cherokee*
– Epigynum without constriction above slender scape (Fig. 14); Canada to southern Mexico. ..... *stellata*

Key to *Acanthepeira* Species, Males

1. Fourth coxa with a tubercle (Figs. 22, 23, 25); whole region 3
– Fourth coxa smooth, not modified (Figs. 24, 26–28); southeastern states 2

2(1) Fourth femur with a proximal, retrolateral tubercle (Fig. 24). ..... *cherokee*
– Fourth femur without such tubercle (Figs. 26–28). ..... *venusta*
3(1) Coxal tubercle large (Fig. 25); on fourth femur, the socket of the proximal, retrolateral macroseta are larger than sockets of more distal macrosetae (Fig. 25); total length 7.0 to 10.4 mm, carapace 3.1 to 4.1 mm wide; southeastern states *marion*
– Coxal tubercle small (Figs. 22, 23); sockets of retrolateral macrosetae of fourth femur about equal in size (Figs. 22, 23); southeastern specimens 6.0 to 8.1 total length, carapace 2.5 to 3.4 mm wide; Canada to southern Mexico. ..... *stellata*

Acanthepeira stellata (Walckenaer)
Plate 3, Figures 12–23, Map 2

Epeira stellata Walckenaer, 1805, Tableau des Aranéides, p. 65. Name for fig. 1, plate 1 of the Bosc manuscript drawings of spiders of Carolina, in the Muséum National d'Histoire Naturelle, Paris. Copy of the illustration in the Museum of Comparative Zoology, examined.

Epeira nobilis Walckenaer, 1841, Histoire Naturelle des Insectes, Aptères, 2: 119. Name for Abbot, fig. 161, p. 16 illustration of a spider from Georgia, in the British Museum, Natural History. Copy in the Museum of Comparative Zoology, examined.

Epeira stellata, – Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 22, pl. 3, fig. 12, ♀. Keyserling, 1863, Sitzungsber. Natur. Ges. Isis, Dresden, 140, pl. 6, figs. 24, 25, ♀. Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 319, pl. 34, fig. 17, pl. 37, figs. 3–5, ♀, ♂. Emerton, 1902, Common Spiders, p. 179, figs. 419, 420, ♀, web.

Acanthepeira stellata, – Marx, 1883, in Howard, List of Invertebrate Fauna of South Carolina, p. 22. Roewer, 1942, Katalog der Araneae, 1: 777. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 234, figs. 714–716, 734, 2038, ♀, ♂, web.

Cyrtarachne dugesi O. P.-Cambridge, 1893, Biologia Centrali-Americana, Araneidea, 1: 113. Female from Guanajuato, Mexico in the British Museum, Natural History, lost.

Cyrtarachne mexicana O. P.-Cambridge, 1893, Biologia Centrali-Americana, Araneidea, 1, pl. 14, fig. 13, ♀ [nomen nudum]. Apparently this illustration belongs with *C. dugesi*.

Marxia stellata, – McCook, 1893, American Spiders, 3: 193, pl. 12, fig. 4, ♀, ♂. F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea 2: 481, pl. 45, figs. 21, 22, ♀. Comstock, 1912, Spider Book, p. 455, figs. 468, 469, ♀, egg sac. Comstock, 1940, The Spider Book, rev. ed., p. 470, figs. 468, 469, ♀, egg sac.

Marxia nobilis, – McCook, 1893, American Spiders, 3. 194, pl. 13, figs. 7–9, ♀, ♂.

Acanthepeira venusta, – Bryant, 1949, Psyche, 56: 175, figs. 4, 5, ♂. Not *A. venusta* Banks.

Araneus stellatus, – Bonnet, 1955, Bibliographia Araneorum, 2(1): 603.

Description of female from Florida. Total length 9.0 mm. Carapace 4.0 mm long, 3.6 wide. First femur, 3.7 mm; patella and tibia, 4.5; metatarsus, 2.9; tarsus, 1.2. Second patella and tibia, 4.2 mm; third, 2.3; fourth, 3.6.

Male from Texas. The abdomen is like that of the female. Total length 8.0 mm. Carapace 4.2 mm long, 3.5 wide. First femur, 3.6 mm; patella and tibia, 4.6; metatarsus, 3.8; tarsus, 1.4. Second patella and tibia, 4.0 mm; third, 2.2; fourth, 3.2.

Variation. Total length of females 7.0 to 15.1 mm, carapace 3.4 to 6.3 long, 3.0 to 5.2 wide. Total length of males 5.1 to 8.1 mm, carapace 2.5 to 4.3 long, 2.0 to 3.4 wide. The first patella and tibia of males is 1.2 to 1.3 times the carapace length. The smallest individuals are from the northernmost localities, the largest southern. While most Florida specimens are intermediate in size, both large and small individuals are found there. Florida specimens are often darker with a light line between the anterior lateral humps, bordering an area that is darker anteriorly, lighter posteriorly. Florida specimens and some others have

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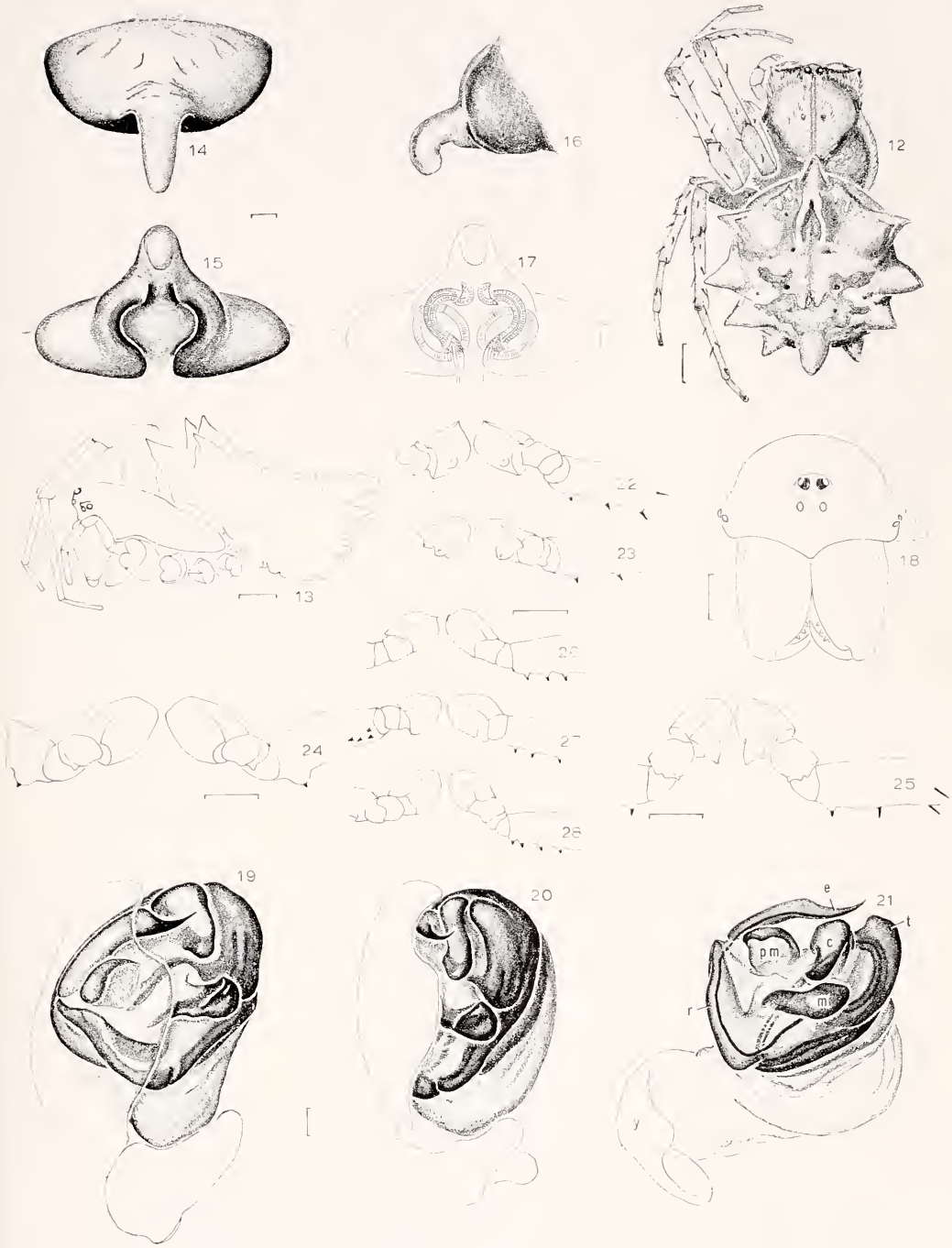
Figures 12–21. *Acanthepeira stellata* (Walckenaer). 12, 13. Female. 14–17. Epigynum. 14. Ventral. 15. Posterior. 16. Lateral. 17. Posterior, cleared. 18. Female, eyes and chelicerae. 19–21. Left palpus. 19. Mesal view, cymbium cleared. 20. Ventral view. 21. Expanded, subventral view.

Figures 22–28. *Acanthepeira* male, fourth coxae and proximal part of fourth femora. 22, 23. *A. stellata*. 24, *A. cherokee*. 25. *A. marion*. 26–28. *A. venusta*.



Abbreviations. c, conductor; e, embolus; m, median apophysis; pm, paramedian apophysis; r, radix; t, tegulum; y, cymbium.

Scale lines. 0.1 mm, except Figs. 12, 13, 22–28, 1 mm.

the scape of the epigynum straight rather than curled, and relatively long, almost as long as the width of the epigynum base. Because individuals with longer scapes were collected with individuals having shorter scapes, and their coloration was the same, matching that of accompanying males of *A. stellata*, I make the assumption that scape length is individually variable and does not indicate different species.

Diagnosis. This is the only species of *Acanthepeira* over most of its range (Map 2). There are, however, three other species in the southeastern states. *Acanthepeira stellata* females differ from those of other species by the relatively small, curled scape of the epigynum (Fig. 14); males by having the tubercle on the fourth coxa (Figs. 22, 23) always present, and by having the bases of the macrosetae on the retrolateral surface of the fourth femur all the same size (Figs. 22, 23). In *A. marion* the most proximal base of the seta is larger. There are specimens that appear intermediate with the smaller *A. venusta* and with the larger *A. marion* (Figs. 46–50).

Natural history. This species is found in meadows and fields and is abundant where found. Specimens have been found in alfalfa and in a cornfield in Ontario, and in Nova Scotia in an apple orchard. They are reported from bayberry bushes (*Myrica* sp.) and sand dunes in Massachusetts; on a sandy beach at Lake Erie, Pennsylvania; in beach, oak and maple woods and on sand in Michigan; in arbor-vitae (*Thuja* sp.) and on a building in Wisconsin. It has been collected by beating soybeans in North Carolina; in an avocado grove in Florida; in low grass in Alabama; by sweeping an old field in Louisiana; on shrubs and tall grass in Texas, and in Georgia from mature beech-magnolia forest (W. Sedgwick, personal correspondence). Comstock (1940) reports the species from low bushes, weeds and grass, with orbs 15 to 25 cm diameter, "hub nearly open, the central space crossed by comparatively few lines; there is a distinct notched zone and a free zone and usually from 20 to 35 viscid spirals. The spider is sometimes found in the orb in midday, but usually rests in a retreat made in the dead head of a plant [which is] one of the supports of the web . . . the mass of eggs is attached to a leaf and enclosed in a mass of loose brown silk (fig. 469)." Kaston (1948) reports 25 radii in the orb and shows a half finished orb (fig. 2038). Males are mature in central and northern states from May to September, females from May to October. *Acanthepeira* have been observed to balloon at 300 m altitude on 13 December (Crosby and Bishop, 1936, J. Entom. Soc. New York, 44: 47).

Distribution. Canada to southern Mexico (Map 2). I have examined juvenile specimens believed to be this species from British Columbia and California, but these are not mapped.

Acanthepeira cherokee n. sp.
Figures 24, 29–35, 42, 43, Map 2

Type. Female holotype from southwest of route 751 at Mud Creek, Durham County, North Carolina, bottomland pine and hardwood forest, 23 September 1964 (J. W. Berry), in the Museum of Comparative Zoology. The name is a noun in apposition, after the southeastern Indian tribe.

Description of female holotype. The humps of the abdomen are relatively low and may be indistinct. Total length 8.3 mm. Carapace 4.3 mm long, 3.9 wide. First

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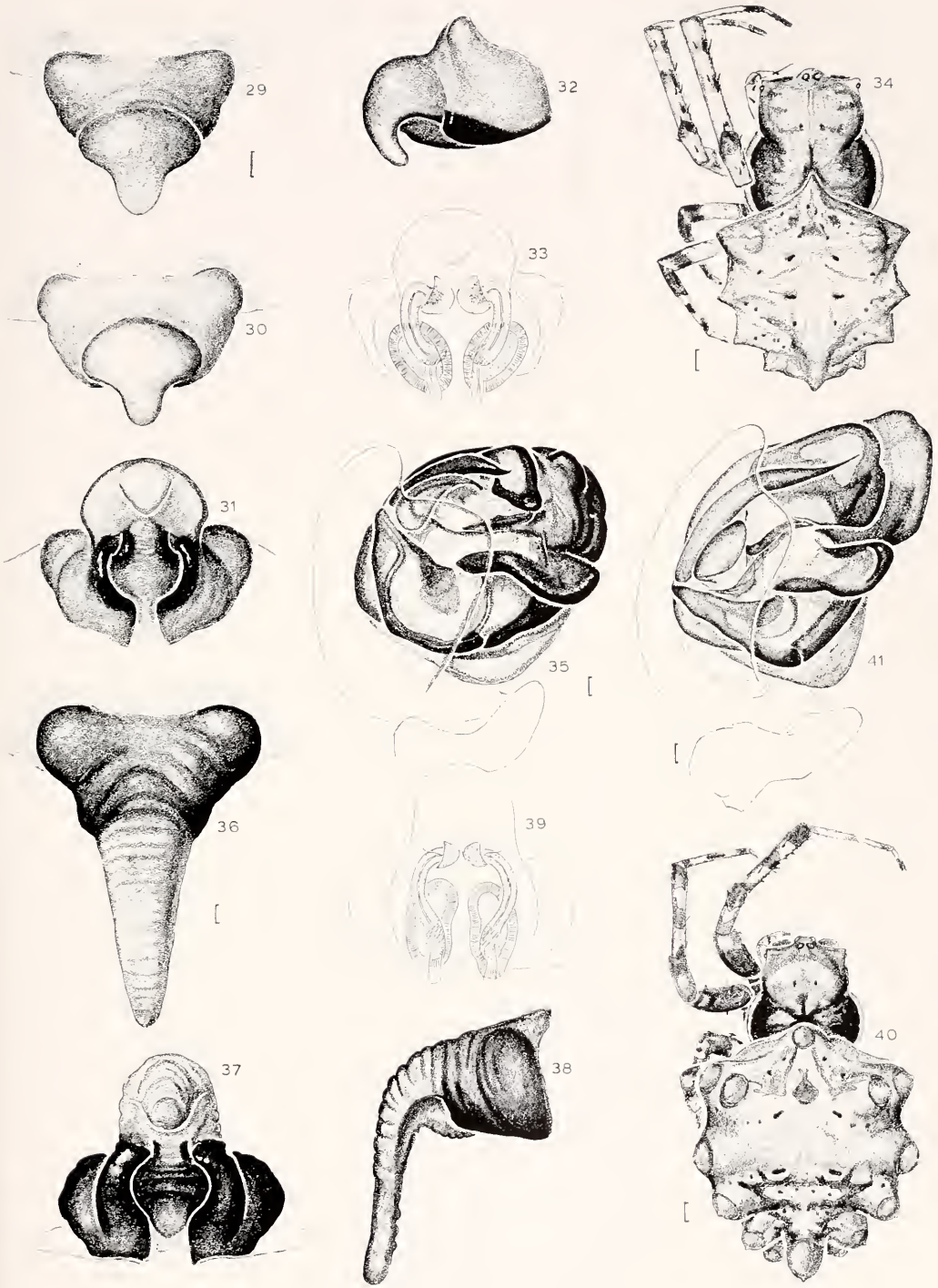
Figures 29–35. *Acanthepeira cherokee* n. sp. 29–33. Epigynum. 29. Anteroventral. 30. Ventral. 31. Posterior. 32. Lateral. 33. Posterior, cleared. 34. Female. 35. Left male palpus, mesal view, cymbium cleared.

Figures 36–41. *A. marion* n. sp. 36–39. Epigynum. 36. Ventral. 37. Posterior. 38. Lateral. 39. Posterior, cleared. 40. Female. 41. Male palpus, mesal view, cymbium cleared.

Scale lines. 0.1 mm, except Figs. 34, 40, 1.0 mm.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femur, 3.4 mm; patella and tibia, 4.6; metatarsus, 2.7; tarsus, 1.4. Second patella and tibia, 4.7 mm; third, 3.0; fourth, 4.0.

Male from Georgia. Total length 11.0 mm. Carapace, 5.2 mm long, 4.1 wide. First femur, 4.1 mm; patella and tibia, 5.6; metatarsus, 3.5; tarsus, 1.4. Second patella and tibia, 5.3 mm; third, 3.4; fourth, 4.7.

Variation. Females vary in total length from 8.3 to 10.4 mm, carapace 4.1 to 4.3 long, 3.5 to 3.9 wide. Male total length 6.5 to 10.9 mm, carapace 3.6 to 5.2 long, 3.0 to 4.1 wide. In males, first patella and tibia is 1.1 times the carapace length. No intermediates were found with other species. One female had an abnormal epigynum (Figs. 42, 43).

Diagnosis. Females differ from those of other *Acanthepeira* species in having low abdominal humps (Fig. 34) and in having a constriction proximal to a swollen area at the base of the short epigynal scape (Figs. 29, 31). Males differ in the lack of tubercles on the fourth coxa, and in the presence of a large tubercle on the base of the fourth femur (Fig. 24). The palpal embolus is shorter and the radix higher than in other species (Fig. 35) and both these structures are hidden by the cymbium.

Natural history. Mature males have been found in February, April and September to November, mature females in March, June, and September. Specimens have been collected in bottomland hardwood by sweeping, bottomland pine and hardwood in North Carolina, at a water reservoir in Illinois, and eating an ant while hanging on a thread in woods around swamp in southern Georgia (W. Sedgwick, personal correspondence).

Distribution. The southeastern states, from Maryland to Missouri, Texas, and Florida (Map 2).

Acanthepeira marion n. sp.
Figures 25, 36–41, 44, Map 2

Type. Female holotype from Marion County, Florida, 21 March 1959 (J. McCrone, B. Mount), in the Museum of Comparative Zoology. The name is a noun in apposition, after the type locality.

Description. Female. The abdomen is encircled by rounded humps that are sometimes slightly sclerotized. Total length 18 mm. Carapace 7.3 mm long, 6.1 wide. First femur, 5.8 mm; patella and tibia, 7.6; metatarsus, 4.0; tarsus, 2.2. Second patella and tibia, 6.9 mm; third, 4.3; fourth, 6.0.

Male from Louisiana. The tips of the abdominal tubercles are more pointed than in the female. Total length 10.4 mm. Carapace, 5.0 mm long, 4.1 wide. First femur, 5.1 mm; patella and tibia, 6.3; metatarsus, 4.1; tarsus, 1.7. Second patella and tibia, 5.4 mm; third, 3.5; fourth, 4.9.

Variation. Females vary in total length from 10.2 to 15.5 mm, carapace 5.1 to 5.9 long, 4.3 to 5.6 wide. Male total length 7.0 to 10.4 mm, carapace 4.1 to 5.0 long, 3.1 to 4.1 wide. In males the first patella-tibia is 1.1 to 1.3 times carapace length. The humps on the abdomen are variable in size and shape. Numerous individuals appear to be intermediate with *A. stellata*, having smaller size, shorter epigynum (Figs. 46, 47) and smaller tubercles on the fourth coxa and femur. The smallest individuals all come from the northernmost localities.

Diagnosis. The long scape of the epigynum (Fig. 36) and the large size of individuals distinguish females from those of other species. The large tubercle on the fourth coxa of males (Fig. 25) and the greater body length is diagnostic for males; some northern *A. stellata* may have large tubercles on the fourth coxae, but specimens from the southeastern states do not. In addition, the base of the most proximal macroseta on the retrolateral surface of the fourth femur is larger than the bases of more distal macrosetae.

Natural history. Specimens have been collected in a field in Illinois, in a sand dune area in Georgia, and by sweeping "old fields" in Louisiana and Florida. Mature males have been collected from March to

June, females from March to August and October.

Distribution. Southeastern states from Pennsylvania to Missouri, Tamaulipas and Florida (Map 2).

Acanthepeira venusta (Banks)
Plate 4, Figures 26–28, 45, 51–56, Map 2

Plectana venusta Banks, 1896, Trans. Amer. Entomol. Soc., 23: 69. One female, two juvenile syntypes from Punta Gorda, Florida in the Museum of Comparative Zoology, examined.

Acanthepeira venusta, – Roewer, 1942, Katalog der Araneae, 1: 777.

Araneus venustus, – Bonnet, 1955, Bibliographia Araneorum, 2(1): 628.

Note. Specimens have usually been called *A. stellata* in collections.

Description. Total length 7.0 mm. Carapace 3.2 mm long, 2.7 wide. First femur, 2.9 mm; patella and tibia, 3.6; metatarsus, 1.7; tarsus, 0.9. Second patella and tibia, 3.1 mm; third, 1.7; fourth, 2.6.

Male. The abdomen is longer than wide. Total length 7.5 mm. Carapace 3.6 mm long, 2.9 wide. First femur, 3.9 mm; patella and tibia, 4.6; metatarsus, 3.0; tarsus, 1.2. Second patella and tibia, 3.8 mm; third, 2.2; fourth, 3.2.

Variation. Total length of Florida females 6–10 mm, carapace 2.2 to 3.9 long, 2.0 to 3.2 wide. The largest female came from Santiago de Cuba and had a total length of 11 mm, carapace 4.5 long, 3.6 wide. Total length of males 4.9 to 7.6 mm, carapace 2.6 to 4.0 long, 1.9 to 3.2 wide. First patella and tibia of males is 1.3 to 1.4 times the carapace length.

Diagnosis. Females of *A. venusta* can readily be separated from those of *A. stellata* by the shape of the epigynum (Fig. 51); the length of the scape is greater than the width of the base, the reverse of the situation in *A. stellata*. Males of *A. venusta* lack the tubercle on the fourth coxa (Figs. 26–28) characteristic of *A. stellata*. Males of *A. cherokee*, which also lack the tubercle on the coxa, have a proximal tubercle on the retrolateral surface of the fourth femur, absent in *A. venusta*. Adults of *A. venusta* are distinguished from other species by their smaller size, by the narrower abdomen (its length 1.5 times its width), and by the longer anterior median tubercle (Fig. 55). (Specimens from Cuba, an area where it is the only *Acanthepeira* species, are larger and have a wider abdomen.) Their lighter, less contrasting coloration and much narrower abdomen make it possible to distinguish juveniles of *A. venusta* from the darker, more deeply colored *A. stellata*, with its rounder abdomen. Some females that could not be separated by epigyna are believed to be intermediates (Figs. 48–50); all have a large epigynum and round abdomen, but the scape is shorter than that of *A. venusta*, smaller and longer than that of *A. stellata*.

Natural history. Acanthepeira venusta can probably be found at all seasons. Specimens have been collected from fields, roadsides, grass, tall grass, grassy cypress (*Taxodium* sp.) and swamp. Several collections came from sawgrass (*Cladium jamaicensis*) in the Everglades. In southern Georgia specimens were found on floating island vegetation in wet places (W. Sedgwick, personal correspondence).

Distribution. Virginia to Florida and Cuba (Map 2).

Wagneriana F.P.-Cambridge

Wagneria McCook, 1893, American Spiders, 4: 203. Type species by monotypy *Epeira tauricornis* O. P.-Cambridge, 1889. Name preoccupied by *Wagneria* Robineau-Desvoidy, 1830, a dipteran; Gistl, 1848, a mollusk; Alenitzin, 1873, a protozoan; Cienkowski, 1882, a protozoan; Jentink, 1886, a mammal; Heilprin, 1887, a mollusk.

Wagneriana F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 497. New name for *Wagneria* McCook, preoccupied. The name is feminine.

Diagnosis. The abdomen of *Wagneriana* differs from that of *Acanthepeira* by lacking the median anterior hump (Fig. 62). The carapace is similar to that of *Acanthe-*

peira in having the head region swollen behind the eyes, but the lateral eye tubercles are rounded (Figs. 62, 63), rather than cone-shaped as in *Acanthepeira*. The clypeus height is about equal to the anterior median eye diameter (Fig. 64). The embolus and median apophysis are more complex in *Wagneriana* than in *Acanthepeira* (Figs. 69–71). In *W. tauricornis*, a piece breaks off the embolus (Figs. 72, 73) during mating and is transferred to the female epigynum. I do not know whether this occurs also in other *Wagneriana* species. The presence of a paramedian apophysis places *Wagneriana* close to *Acanthepeira*, *Parawixia* and *Eriophora*. *Wagneriana* differs from the last two genera by the shape of the carapace, especially the swollen head region (Figs. 62–64).

Genitalia. The epigynum has the small median scape attached broadly to the base; the scape is not annulate (Figs. 57–59). The openings, as in all members of this group of genera, are on the posterior face in a slit (Fig. 59). The seminal receptacles are dumbbell-shaped (Fig. 61).

The median apophysis in the palpus is a huge sclerite facing the ventral side, its structure differing in different species (Figs. 69, 70). The conductor supports the complex embolus (Fig. 71). The embolus has two lateral flat branches, unlike that of *Acanthepeira*, and the lower one bears a scale that breaks off and lodges in the opening of the epigynum (Figs. 59, 72, 73).

Coloration. Head region light, thorax brown, sides of thorax black, chelicerae mottled, darker distally. Sternum dark, coxae mottled, legs with narrow bands. Dorsum of abdomen mottled black, brown, and white (Fig. 62). Tubercles white on tips. Sides mottled. Epigastric area black. Dark behind epigynum, lighter on sides and posteriorly in front of spinnerets. There is a thin black line around spinnerets on venter. Color of males like that of females.

Structure. Head region of carapace swollen, lateral eyes separate from medians on a shared tubercle (Figs. 63, 64). The height of the clypeus equals the diameter of the anterior median eyes (Fig. 64). The abdomen is soft, longer than wide, with large tubercles (Figs. 62, 63, 65, 66).

The male is slightly smaller than the female, and similar in shape, except that the carapace is narrower in the region of the anterior median eyes (Fig. 67). The thorax has a median longitudinal line and median eyes more anterior to lateral eyes than in female. The palpal femur lacks a distinct proximal tooth. The palpal patella has one macroseta. The first coxa has a distal hook. The second tibia is slightly swollen and may have macrosetae.

Species. There are several Central and South American species which differ considerably from each other both in size and structure of the genitalia.

Distribution. The genus is known from the Americas only. One species extends into the temperate area. Records of *W. undecimaculata* from the United States are in error.

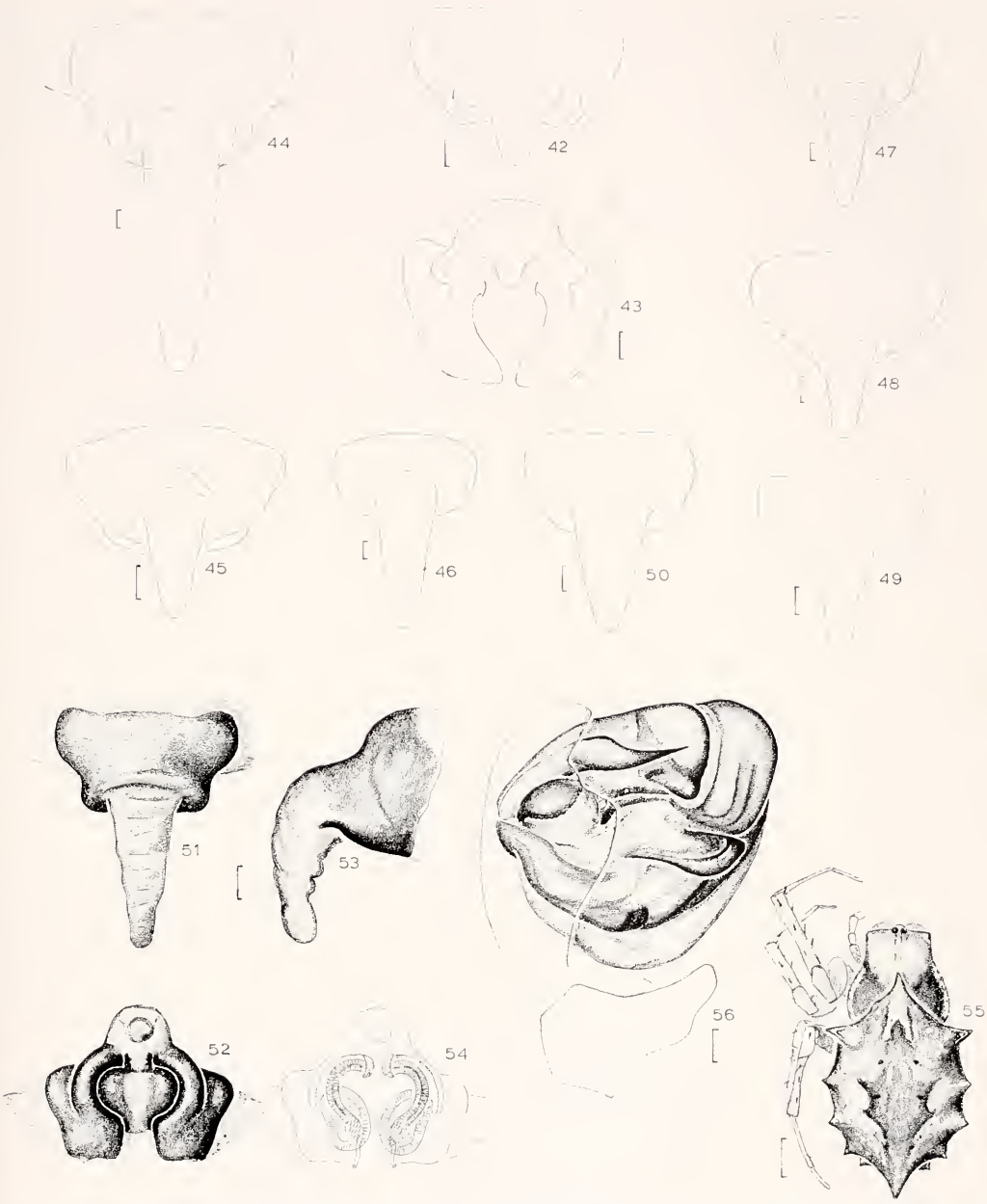
Wagneriana tauricornis (O.P.-Cambridge) Figures 57–73, Map 3

Epeira tauricornis O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 44, pl. 6, figs. 2, 3, ♀, ♂. Many syntype specimens without locality data from numerous localities (as published) in Guatemala and Bugaba and Volcan de Chiriquí, Panama, in the British Museum, Natural History, examined. Keyserling, 1892, Spinnen Amerikas, 4: 90, pl. 4, fig. 68, ♂.

Epeira guatemalensis O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidae, 1: 40, pl. 7, fig. 8, ♂ (not ♀). Male syntypes from numerous localities in Guatemala. Keyserling, 1892, Spinnen Amerikas, 4: 112, pl. 6, fig. 83b, ♂ (not ♀).

Wagneria tauricornis, – McCook, 1893, American Spiders, 3: 204, pl. 13, fig. 1, 2, ♀, ♂.

Wagneriana tauricornis, – F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 498, pl. 47, figs. 14, 15, ♀, ♂. Comstock, 1912, Spider Book, p. 460, fig. 473, ♀; 1940, rev. ed., p. 474, fig. 473, ♀. Roewer, 1942, Katalog der Araneae, 1: 881. Bonnet, 1959, Bibliographia Araneorum, 2(5): 4803.



Figures 42–50. Variation of *Acanthepeira* epigyna. 42, 43. *A. cherokee* (Georgia). 42. Ventral. 43. Posterior. 44. *A. marion* (Mississippi). 45. *A. venusta* (Baldwin Co., Alabama). 46–50. Doubtful, intermediate specimens. 46, 47. *A. marion–stellata*. 46. (Monroe Co., North Carolina). 47. (Everglades, Florida). 48–50. *A. stellata–venusta*. 48. (Chihuahua). 49. (North Wales, Pennsylvania). 50. (Osceola, Florida).

Figures 51–56. *Acanthepeira venusta* (Banks). 51–54. Epigynum. 51. Ventral. 52. Posterior. 53. Lateral. 54. Posterior, cleared. 55. Female. 56. Left male palpus, mesal view, cymbium cleared.

Scale lines. 0.1 mm, Fig. 55, 1 mm.

Map 3. Distribution of *Wagneriana tauricornis* (O.P.-Cambridge).

Description of female from Florida. Sternum black, coxae mottled. Posterior median and lateral eyes subequal to anterior medians, anterior lateral eyes 0.8. Anterior median eyes slightly more than their diameter apart, posterior median eyes their diameter apart. The chelicerae have four teeth on the anterior margin, two on the posterior. Total length 6.0 mm. Carapace 2.2 mm long, 1.7 wide. First femur, 2.2 mm; patella and tibia, 2.6; metatarsus, 1.4; tarsus, 0.7. Second patella and tibia, 2.1 mm; third, 1.2; fourth, 2.0.

Male from Florida. Median eyes subequal in size, laterals 0.8 diameter of medians. Anterior median eyes their diameter apart, posteriors their diameter apart. Second tibia is slightly swollen with macrosetae. The male has fewer and more distinct abdominal tubercles than the female (Fig. 67). Total length 5.8 mm. Carapace 2.6 mm long, 1.8 wide. First femur, 2.4 mm; patella and tibia, 2.8; metatarsus, 1.6; tarsus, 0.7. Second patella and tibia, 2.1 mm; third, 1.5; fourth, 1.9.

Variation. Total length of females varies 4.3 to 6.1 mm; carapace 1.9 to 2.5 long, 1.5 to 2.0 wide. Total length of males 3.3 to 5.8 mm; carapace 2.0 to 2.6 long, 1.6 to 2.0 wide. All the smallest specimens came from Florida. The shape of the abdomen, especially tail length, is much more variable in Central America (Figs. 65, 66) than in southeastern United States. Central American females may have the epigynum in slightly different proportion, the scape wider or narrower.

Diagnosis. Wagneriana tauricornis is smaller than related Central and South American *Wagneriana*. Females can be distinguished from all related species by the constricted neck of the scape of the epigynum (Fig. 57), males by the shape of the embolus and median apophysis of the palpus (Figs. 69, 70) and the macroseta on the fourth trochanter (Fig. 68).

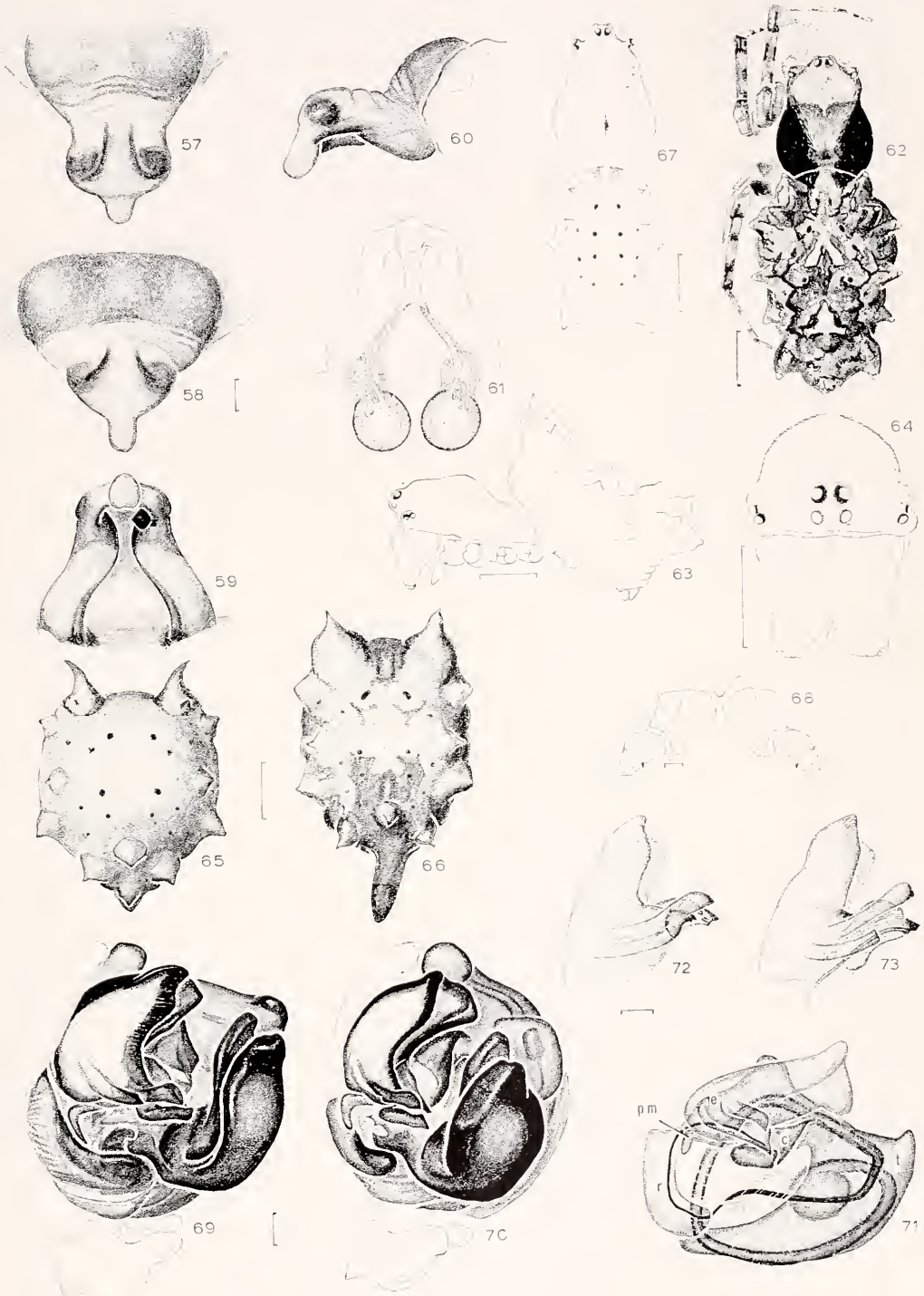
Natural history. Specimens have been found on shrubs and trees, by sweeping hophornbeam (*Ostrya virginiana*), on a hammock, in a banana farm, in a swamp, in weeds bordering stream in Florida, and on bromeliads in Mexico. Comstock (1940) writes that a specimen "held its legs closely folded when hanging in its web;" and that when in this position, it looked like a bit of dirt. Archer (1940) indicates that vertical webs are found 1.8 m off the ground on shrubs and trees along streams, ravines and swamp woods. Mature females have

→

Figures 57–73. *Wagneriana tauricornis* (O.P.-Cambridge). 57–61. Epigynum. 57. Anterior. 58. Ventral. 59. Posterior. 60. Lateral. 61. Posterior, cleared. 62. Female (Florida). 63. Female, lateral. 64. Female eye region and chelicerae. 65, 66. Female abdomens (Guatemala). 67. Male carapace and abdomen. 68. Male, fourth coxae and trochanter. 69–73. Left male palpus. 69. Mesal view. 70. Ventral view. 71. Palpal bulb expanded with median apophysis cut off in subventral view. 72. Embolus with cap. 73. Embolus without cap.

Abbreviations. c, conductor; e, embolus; pm, paramedian apophysis; r, radix; t, tegulum.

Scale lines. 0.1 mm, except Figs. 62–67, 1 mm.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been collected in March, and from August to December in Florida, males in February, March, July, October, and in December in Florida. Details of the web are not known.

Distribution. Georgia, Texas to South America (Map 3).

Acacesia Simon

Acacesia Simon, 1895, Histoire Naturelle des Araignées, 1: 795. Type species by original designation and monotypy *Epeira foliata* Hentz (= *E. hamata* Hentz). The name is feminine.

Diagnosis. Acacesia is close to *Wixia.* It differs from *Araneus* and most other genera by the narrow head region and the swollen, bulging area between the median eyes (Fig. 80). The second eye row is strongly recurved, the posterior median eyes anterior to the anterior laterals, and directed sideways rather than dorsally (Figs. 78–80). The anterior median eyes are largest, the ocular quadrangle wider in front than behind. The laterals are separated by almost their diameter. Only in *Wixia* is the eye area similar, and *Acacesia* differs from *Wixia* by the oval shape of the abdomen and its characteristic dorsal pattern present in all species (Figs. 78, 81). The legs are relatively longer than in other genera of this group (Figs. 78, 81).

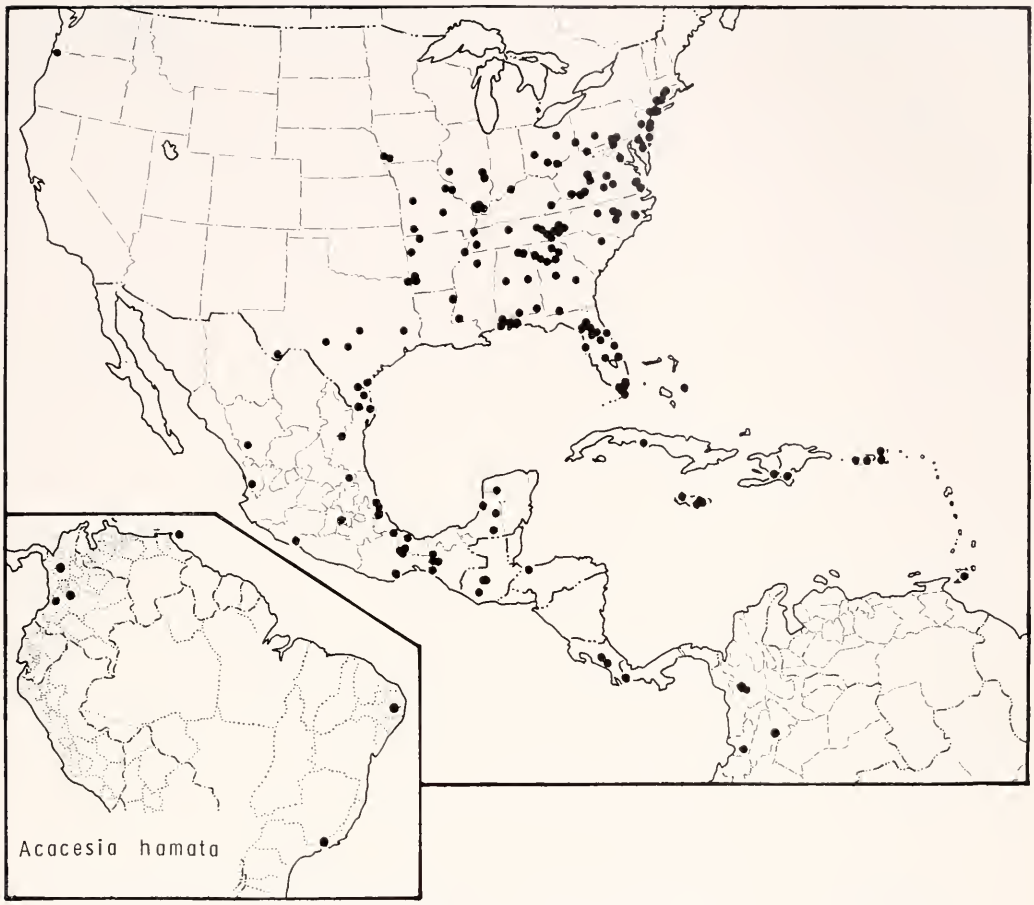
Genitalia. The female epigynum has the scape set off from the base. The scape is flat, not annulate and the openings are in slits on the posterodorsal side (Figs. 74–77). The palpus has a complex embolus resting on a short conductor (Figs. 82, 84). As in other genera of this group, the conductor (c in Fig. 84) faces mesally rather than ventrally as in *Araneus.* The median apophysis is huge (m in Fig. 84). There is a lamella mesal to the embolus, perhaps a terminal apophysis (a). A small scale breaks off the embolus during mating and remains in the epigynum (Fig. 75). There is no paramedian apophysis. In *Acacesia* alone among related genera the paracymbium is modified, and not simply hook-shaped (Fig. 83).

Coloration. Carapace, sternum and legs brown; legs not banded. All known species have the same dorsal abdominal pattern: four black lines, the inner ones approaching each other anteriorly and joining posteriorly in the middle of the abdomen; the outer lines join anteriorly and approach each other above the spinnerets. The lines are laterally bordered by a white line (Figs. 78, 81). The area between the lines is darker brown than the color on the sides. Anterolateral is a dark gray patch that continues posteriorly into the dark brown sides. Sides are sharply delimited toward lighter dorsum, but grade into lighter venter. There are no distinct marks on venter. Area between genital groove and spinnerets is darker than sides. Coloration of male deeper (Fig. 81).

Structure. Head area of carapace narrow, eyes closely grouped with posterior median eyes directed sideways as result of swelling of median eye area (Figs. 79, 80). Clypeus height subequal to diameter of anterior median eyes. The legs are long, the first patella-tibia about 1.7 times carapace length with hardly any macrosetae. The leg length order is 1, 2, 4, 3 (Figs. 78, 81). The abdomen is suboval, longer than wide, widest in anterior half and without humps (Fig. 78).

Males slightly smaller than females. Thorax with a shallow circular depression, traversed by a longitudinal median line. Head and clypeus height as in female (Fig. 81). The palpal femur has a tooth facing a tooth on the endite. The palpal patella has one macroseta. The first coxa has a large distal hook that fits into a groove on the second femur. The second leg has a ventral row of setae on the femur and a spur on the tibia (Fig. 87). The fourth coxa has a short stout macroseta, as does the fourth trochanter (Fig. 86).

Species. Only one species, *Acacesia hamata,* occurs in our region. But there are three or four additional species of *Acacesia,* all Neotropical and all similar in appearance. Juveniles thus can be determined



Map 4. Distribution of *Acacesia hamata* (Hentz).

only north of Mexico. The genitalia of females differ in proportions and amount of sclerotization. Palpi of males differ in the shape of the embolus, but all have a huge biforked median apophysis, slightly narrower in other species than in *A. hamata*.

Acacesia hamata (Hentz)
Plate 5, Figures 74–87, Map 4

Epeira ? hamata Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 474, pl. 31, fig. 10, ♂. Male type from Alabama in the Boston Soc. Natur. Hist., destroyed.

Epeira foliata Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 475, pl. 31, fig. 14, ♀. Female type from Alabama in the Boston Soc. Natur. Hist., destroyed. (Not *Epeira foliata* C. L. Koch, 1845.) Emerton, 1884, Trans. Connecticut Acad. Sci., 6: 318, pl. 34, fig. 10, pl. 37, figs. 6–10, ♀, ♂. McCook, 1894, American Spiders, 3: 154, pl. 4, figs. 7, 8, ♀, ♂. F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 502, pl. 48, figs. 1, 2, ♀, ♂.

Epeira folifera Marx, 1890, Proc. U. S. Natl. Mus., 12: 545, 593. New name for *foliata* Hentz, preoccupied.

Acacesia foliata, – Comstock, 1912, Spider Book, p. 509, figs. 546–548, ♀. Comstock, 1940, Spider Book, rev. ed., p. 522, figs. 546–548, ♀. Bonnet, 1955, Bibliographia Araneorum, 2. 122.

Acacesia folifera, – Roewer, 1942, Katalog der Araneae, 1: 763.

Acacesia hamata, – Bryant, 1945, Bull. Mus. Comp. Zool., 95: 364. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 235, fig. 705, figs. 725–726, ♀, ♂.

Note. The name *A. hamata* has been used for this common species since Bryant, 1945. Hentz's 1847 description is not very specific and the type is destroyed. However, Hentz's unpublished original colored illustration at Harvard University with outline of palpus and second leg with added description leaves no doubt that he applied *E. hamata* to a male of this species.

Description of female from Everglades, Florida. Posterior median eyes 0.9 diameter of anterior medians, lateral eyes 0.6 diameter. Anterior median eyes 1.5 diameters apart, 1.8 from laterals; posterior medians 1.3 diameters apart, 2.2 from laterals. There are four long teeth on the anterior margin of the chelicerae, three on the posterior, denticles between. Total length 6.3 mm. Carapace 2.7 mm long, 2.0 wide. First femur, 4.1 mm; patella and tibia, 4.8; metatarsus, 3.5; tarsus, 1.2. Second patella and tibia, 4.3 mm; third, 1.8; fourth, 3.0.

Male from Georgia. Carapace with one macroseta behind each lateral eye. Swollen area between median eyes bearing a pair of setae. Posterior median eyes 0.6 diameter of anterior medians, laterals 0.4 diameter. Anterior median eyes their diameter apart, their diameter from laterals. Posterior median eyes slightly more than their diameter apart, 2.2 from laterals. Total length 4.8 mm. Carapace 2.1 mm long, 1.8 wide. First femur, 3.5 mm; patella and tibia, 3.7; metatarsus, 2.7; tarsus, 0.8. Second patella and tibia, 2.7 mm; third, 1.4; fourth, 2.2.

Variation. Females measure total length 4.7 to 9.1 mm, carapace 2.1 to 2.9 long, and 1.7 to 2.7 wide. Males, total length 3.6 to 4.8 mm, carapace 1.9 to 2.2 long, 1.6 to 1.8 wide. The largest specimens come from Texas and Mexico.

Diagnosis. This is the only species of *Acacesia* north of Mexico. *Acacesia hamata* differs from the similar, sympatric *A. cornigera* Petrunkevitch, the common species of Central America and northern South America, and from other species found in Mexico, by the proportions of the genitalia. In *Acacesia hamata* the scape of the epigynum has a constricted neck and is shorter than the width of the base (Fig. 74); it is the reverse in *A. cornigera.* The male palpus has the median apophysis higher (Fig. 82) than long and also has a small distal spine parallel to the part bearing the embolic duct (Fig. 85). This spine is absent in other species that have the median apophysis longer than high.

Natural history. I have collected the species by sweeping shrubs in a cranberry bog in the pine-barrens of New Jersey. It has also been found in bottomland pine-hardwood in North Carolina, floodplain in Louisiana, and second growth oak-hickory woods in Missouri. In northern states males are mature from late July until early September and mature females can be found from late June until September. In the tropics males have been found in various months. In Florida, mature females were found in November, December and March.

J. E. Carico provided information on the webs of ten females observed in Virginia (in letter). Webs are built in tall weeds, 1.2 to 1.5 m from the ground. Two webs were found in low branches of trees at the margin of a lawn. The web is made precisely at sundown. Web is removed at sunrise. No exceptions to this were observed. All females made a web every evening. The spiders remained in the hub during the night, head down with legs partly extended (Plate 5). The webs averaged 33 radii and 118 spirals. The structure is very fine and dense with spirals close together. Photographing the web is difficult because adjacent spirals stick together under the weight of flour particles used in making it visible (Plate 5). The outline of the web is triangular. No retreat is made. The spider "rests" in a different location in vegetation each day, usually within six inches of the last resting place (Plate 5). Web is located differently each evening.

Distribution. Eastern United States from Connecticut to Iowa, south to Florida, Texas and to northern Brazil (Map 4).

Figures 74–87. *Acacesia hamata* (Hentz). 74–77. Epigynum. 74. Ventral. 75. Posterior. 76. Ventral cleared. 77. Posterior cleared. 78. Female, dorsal. 79. Female, lateral. 80. Female eye region and chelicerae. 81. Male. 82–85. Male left palpus. 82. Mesal. 83. Ventral. 84. Expanded. 85. Embolus. 86. Fourth coxae and trochanters. 87. Second left leg, prolateral.

Abbreviations. a, terminal apophysis; c, conductor; e, embolus; m, median apophysis; r, radix; t, tegulum.

Scale lines. 0.1 mm; except Figs. 78–81, 1.0 mm.

Wixia O.P.-Cambridge

Wixia O. P.-Cambridge, 1882, Proc. Zool. Soc. London, p. 437. Type species by monotypy *Wixia abdominalis* O. P.-Cambridge. The name is feminine.

Ocrepeira Marx, 1883, in Howard, List of Invertebrates of South Carolina, 11: 22. Type species by monotypy *Epeira ectypa* Walckenaer.

Amamra O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 55. Type species by monotypy *A. bituberosa* O. P.-Cambridge, 1889.

Notes. Wixia abdominalis is a South American species known from juvenile specimens only. Neave (1939) does not list *Ocrepeira*, perhaps because Marx failed to indicate that he was introducing a new name.

Diagnosis. Wixia differs from other genera included in this paper by having the abdomen at an angle to the cephalothorax (Fig. 107), as in *Mangora*, but *Mangora* has trichobothria on the third tibia and *Wixia* does not. *Wixia* differs from *Scoloderus* by the low cephalothorax (Fig. 92). Sometimes the anterior part of the abdomen is extended and projects up. Like *Acacesia*, *Wixia* has the posterior median eyes well separated and directed laterally rather than dorsolaterally, the area between appearing swollen (Figs. 92, 105). Unlike other genera including *Acacesia*, *Wixia* has the clypeus almost as high as two diameters of the anterior median eyes, and the legs are short and thick (Figs. 92, 105).

Genitalia. The epigynum is a heavily sclerotized structure with a wide posterior-facing lobe in ventral view. The ventral view and shape of the abdomen are variable within species. The posterior view is diagnostic for species determination (Figs. 89, 102, 117). The seminal receptacles are oval with an atrium between them and the opening. Into the atrium opens a lobe with a seemingly spiral lumen (Figs. 91, 104, 119).

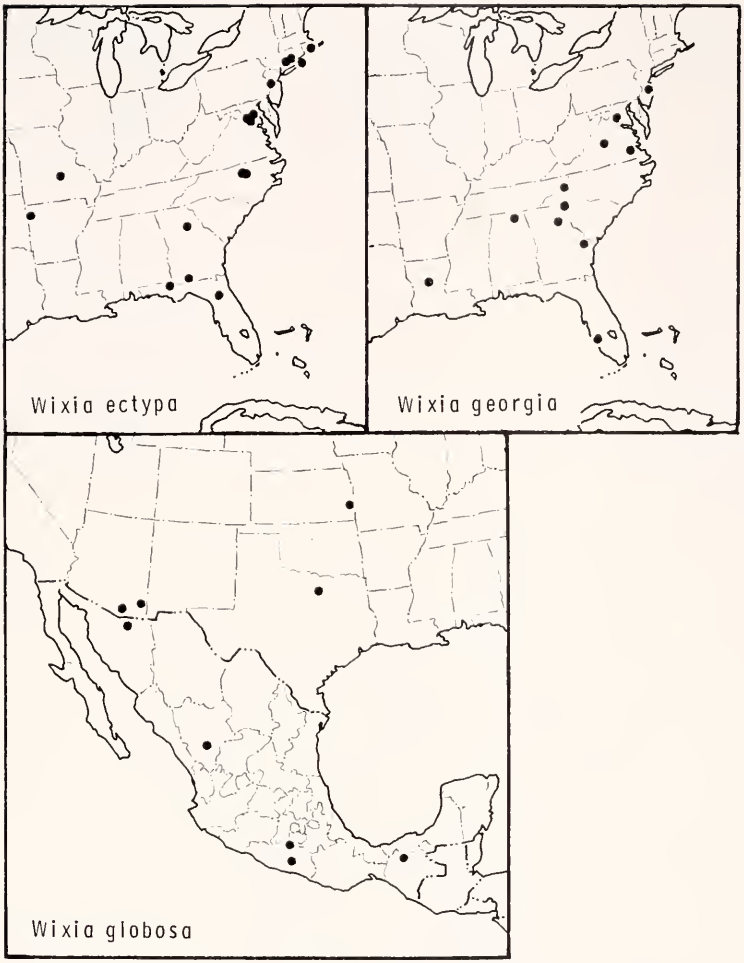
The median apophysis of the palpus (m in Figs 98, 99) is an enormous structure with a long distal prong at right angles to the long axis of the palpus (Figs. 97, 109, 122). The paramedian apophysis is a basal lobe of the conductor (c in Figs. 98, 99). The terminal apophysis (a), an E-shaped structure lying above the embolus and hardly separated from it (Figs. 113–115), is diagnostic.

Coloration. Similar in all species north of Mexico. Carapace brown with black marks and light setae, but no hair between median eyes. Distal half of chelicerae darker than basal half. Sternum brown with darker borders. Coxae light, distal parts of legs banded more distinctly dorsally than ventrally; legs darker dorsally than ventrally. Abdomen mottled dorsally with two transverse black marks whose lateral ends point anteriorly (Figs. 93–95). Sides and venter gray.

Structure. Height of clypeus 1.5 to 2 diameters of anterior median eyes. Median eye area swollen, and posterior median eyes facing laterally. Posterior median eyes slightly larger to 1.4 times diameter of anterior medians, laterals about 0.8 diameter of anterior medians. The anterior median eyes are one to two diameters apart, as are the posterior medians. The legs are heavy, short and setose (Fig. 105); the first patella-tibia is 1.0 to 1.2 times carapace length in both sexes. The hairy abdomen is attached at an angle to the cephalothorax and its shape is variable within species, having one median anterior hump, two humps, or none.

Males are only slightly smaller than females and do not have longer legs. The thorax has a median longitudinal line with a transverse branch pointing anteriorly in the midline. The femur of the palpus has a proximal tooth, the palpal patella one macroseta. The first coxa has a distal lateral hook and the second femur a groove. The second tibia is swollen and has strong macrosetae (Figs. 110–112); the patella has a slit on the posterior side. The first femur has on the venter, distally a line of macrosetae, the second femur has a complete line of macrosetae.

Natural history. All three species are rarely collected but are found in wasp



Map 5. Distribution of *Wixia* species found north of Mexico.

nests (Levi, 1973). They probably make their unknown orbs in trees and rest at daytime appressed to twigs.

Species. There are three species north of Mexico, of which only mature individuals can be determined, on the basis of differences in genitalia; the abdomen is variable within species. There are perhaps six additional species in tropical America, none in other parts of the world.

KEY TO FEMALE *WIXIA*

1. Openings on side of epigynum (Figs. 89, 91). ..... *ectypa*
– Openings posteriorly on epigynum (Figs. 102, 104, 117, 119). 2
2(1) Epigynum with a deep transverse groove posteroventral to posterior median lobe, seen on upper part of Fig. 117. ..... *globosa*
– Epigynum slightly swollen posteroventral to posterior median lobe, Fig. 103 and seen on upper part of Fig. 102. ..... *georgia*

KEY TO MALE *WIXIA*

1. Terminal apophysis, E-shaped in Figs. 108, 114, 115, 121, with "bottom" and "top" prong subequal in size. 2
– Terminal apophysis with "top" prong much larger than "bottom" prong (Figs. 96, 113). ..... *ectypa*
2(1) Middle prong of terminal apophysis

shorter than other two (Fig. 115); long prong of median apophysis with diameter one-third height of median apophysis (Fig. 122). ..... *globosa*

– Middle prong of terminal apophysis as long as other two (Fig. 114); long prong of median apophysis with diameter less than one-quarter height of median apophysis (Fig. 109). ..... *georgia*

Wixia ectypa (Walckenaer)

Figures 88–100, 110, 113, 123, Map 5

Epeira ectypa Walckenaer, 1841, Histoire Naturelle des Insectes Aptères, 2: 129. Types are figs. 143 and 144 of Abbot's manuscript illustrations of Georgia spiders, in the British Museum, Natural History, copy of manuscript in Museum of Comparative Zoology, examined. Keyserling, 1863, Sitzungsber. Naturwiss. Isis Dresden. p. 135, pl. 6, figs. 13–16, ♀, ♂.

Epeira infumata Hentz, 1850, J. Boston Soc. Natur. Hist., 6: 19, pl. 3, fig. 4, ♀. Female types from North Carolina and Alabama in the Boston Natural History Society, destroyed. Emerton, 1884, Trans. Connecticut Acad. Sci. 6: 319, pl. 37, figs. 11–13, ♀.

Ocrepeira ectypa, – Marx, 1883, in Howard, List of Invertebrates of South Carolina, 11: 22.

Wixia ectypa, – Keyserling, 1892, Spinnen Amerikas, 4: 46, pl. 2, fig. 38, ♀, ♂. McCook, 1893, American Spiders, 3: 205, pl. 13, figs. 4, 5, ♀, ♂. Comstock, 1912, Spider Book, p. 467, fig. 481, ♀; 1940, rev. ed., p. 481, fig. 481, ♀. Roewer, 1942, Katalog der Araneae, 1: 882. Kaston, 1948, Bull. Connecticut Geol. Natur. Hist. Surv., 70: 230, figs. 728–730, ♀. Bonnet, 1959, Bibliographia Araneorum, 2: 4828.

Wixia anaclyphe, – Chamberlin and Ivie, 1944, Bull. Univ. Utah. Biol. Ser., 8(5): 115. Archer, 1951, Amer. Mus. Novitates, no. 1487, figs. 50, 54, ♀ (error in determination, not *Epeira anaclyphe* Walckenaer).

Wixia hentziana Archer, 1951, Amer. Mus. Novitates, no. 1487, figs. 48, 52, ♀. Female holotype from Florida [no locality] in the American Museum of Natural History, examined. NEW SYNONYMY.

Note. Although Abbot's illustration of the type of *E. ectypa* is not species diagnostic, and neither is that of Hentz, the old specimens which were examined and used by Keyserling and Emerton were of this species and not the species here called *W. georgia*.

Chamberlin and Ivie (1944) used the name *Wixia anaglyphe* for this species. *Epeira anaglyphe* Walckenaer, 1805, Tableau des Aranéides, p. 58, with the type Bosc's manuscript illustration, plate 5, no. 6 (labeled "*Aranea hamata*") of the spiders of Carolina in the Muséum National d'Histoire Naturelle, Paris (copy of plate in the Museum of Comparative Zoology, examined) is a *Mimetus*, Mimetidae, and certainly not this species. In an 1841 citation Walckenaer (Histoire Naturelle Insectes Aptères, 2: 12) also cites Abbot's figure 349 to be *Epeira anaglyphe*. This, unlike the Bosc drawing, appears to be a *Wixia*. The type of Archer's *W. hentziana* is a large specimen, its abdomen twice the length of the Georgia ones illustrated, but the epigynum hardly differs in size or shape.

Description. Female. Total length 5.2 mm. Carapace 2.8 mm long, 2.5 wide. First femur, 2.7 mm; patella and tibia, 3.3; metatarsus, 2.0; tarsus, 0.8. Second patella and tibia, 3.2 mm; third, 2.0; fourth, 3.0

Male. Total length 6.1 mm. Carapace 4.1 mm long, 3.4 wide. First femur, 3.8 mm; patella and tibia, 4.7; metatarsus, 2.3; tarsus, 0.9. Second patella and tibia, 4.0 mm; third, 2.7; fourth, 3.7.

Variation. The abdomen is quite variable in shape (Figs. 93–95). Females vary total length 5.2 to 9.4 mm, carapace 2.8 to 3.5 long, 2.2 to 3.0 wide. Males vary total length 5.4 to 7.2 mm, carapace 3.5 to 4.0 long, 3.0 to 3.7 wide.

Diagnosis. Females differ from *W. georgia* and *W. globosa* by having the openings of the epigynum lateral (Figs. 89–91) rather than posterior. Males have the width of the distal prong of the E-shaped terminal apophysis one-third to one-half the height of the whole structure (Fig. 96), its width is less than one-quarter the height in *W. globosa* and *W. georgia*.

Natural history. This is the most common species. Perhaps half the specimens in collections come from wasp nests (*Trypoxylon* sp.), some came from sweeping mesic to bottomland woods; another one was found on a fence, "mimicking bud on

Figures 88–100. *Wixia ectypa* (Walckenaer). 88–91. Epigynum. 88. Ventral. 89. Posterior. 90. Lateral. 91. Posterior, cleared. 92. Female, eye region and chelicerae. 93–95. Female abdomen, posterior. 93. (Florida). 94, 95. (Georgia). 96–100. Left male palpus. 96. Mesal. 97. Ventral. 98–100. Expanded. 98. Mesal. 99. Subventral. 100. Embolus, dorsal.

Abbreviations. a, terminal apophysis; c, conductor; e, embolus; h, hematodocha; m, median apophysis; pm, paramedian apophysis; p, paracymbium; t, tegulum; y, cymbium.

Scale lines. 0.1 mm; Figs. 92–95, 1 mm.

cedar twig" (*Chamaecyparis* sp.); one was found "on house." Mature females have been collected from July to November, males from September to December.

Distribution. Massachusetts, Missouri, to Florida. The northernmost locality is Woods Hole, Massachusetts, but the specimens are juvenile and could be another species (Map 5).

Wixia georgia n. sp.
Figures 101–109, 111, 114, 124, Map 5

Type. Male holotype from a wasp trap, 8 June 1969, Athens, Clarke Col., Georgia (R. and J. Matthews) in the Museum of Comparative Zoology. The specific name is a noun in apposition after the state of the type locality.

Description. Female from Georgia. Posterior median eyes 1.2 diameters of anterior medians; anterior laterals 0.6 posterior laterals 0.7 diameters. The lateral eyes are slightly separated from each other. Anterior median eyes two diameters apart, posterior medians one diameter. Total length 6.5 mm. Carapace 3.5 mm long, 3.0 wide. Abdomen 5.3 mm long. First femur, 2.9 mm; patella and tibia, 3.5; metatarsus, 2.3; tarsus, 0.9. Second patella and tibia, 3.4 mm; third, 2.2; fourth, 3.5.

Male holotype. Posterior median eyes same diameter as anterior medians; laterals 0.5 diameter. Anterior median eyes 1.6 diameters apart, posterior median eyes two diameters apart. The laterals are slightly separated. The height of the clypeus is 1.5 diameters of the anterior median eye. Each third and fourth coxa and trochanter has a single ventral macroseta, a large one on the fourth, a small one on the third (Fig. 124). The first femur has a distal row of ventral macrosetae, the second and fourth a complete ventral row of macrosetae The second tibia is swollen (Fig. 111). Total length 5.3 mm. Carapace 2.9 mm long, 2.4 wide. First femur, 2.9 mm; patella and tibia, 3.5; metatarsus, 1.9; tarsus, 0.9. Second patella and tibia, 2.9 mm; third, 1.7; fourth, 2.8.

Variation. The abdomen is variable in shape. Total length of females 5.8 to 7.3 mm; carapace 3.0 to 3.5 long, 2.3 to 3.0 wide. Total length of males 4.0 to 6.0 mm; carapace 2.6 to 3.0 long, 1.9 to 2.4 wide.

Diagnosis. *Wixia georgia* female differs from that of *W. globosa* in having the area behind the posterior lip of the epigynum swollen (Figs. 102, 103), from that of *W. ectypa* by having the openings on the posterior face (Fig. 102) rather than on the sides. The male differs from that of *W. ectypa* by having the distal prong of the E-shaped terminal apophysis thinner, from that of *W. globosa* by having the middle prong longer and thinner and the embolus a different shape (Figs. 108, 114).

Natural history. Most specimens come from wasp collections. Mature females have been collected from May to August, males from May to June.

Distribution. From New Jersey to Louisiana and Florida (Map 5).

Wixia globosa F.P.-Cambridge
Figures 112, 115–122, 125, Map 5

Amaura clivosa O. P.-Cambridge, 1898, Biologia Centralia Americana, 1: 270, pl. 36, fig. 2, ♂. Male paralectotypes, not female lectotype, here designated. Female lectotype is *W. rufa*.

Wixia clivosa, – F. P.-Cambridge, 1904, Biologia Centrali Americana, 2: 485, pl. 46, fig. 2, ♂ (not fig 3, ♀).

Wixia globosa F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 486, pl. 46, fig. 4, ♀. Female holotype from Tepetlapa, [Oaxaca], Mexico in the British Museum, Natural History, examined.

Wixia bryanti Archer, 1951, Amer. Mus. Novitates, no. 1487: 16, fig. 33, ♀. Female holotype from White House Canyon, Santa Rita Mts., Arizona, in the American Museum of Natural History, examined. NEW SYNONYMY.

Description. Female. Total length 5.8 mm. Carapace 2.5 mm long, 2.3 wide. First femur, 2.3 mm; patella and tibia, 3.0; metatarsus, 1.9; tarsus, 0.7. Second patella and tibia, 2.9 mm; third, 1.7; fourth, 2.8.

Male. Total length 5.0 mm. Carapace 3.7 mm long, 2.5 mm wide. First femur, 2.9 mm; patella and tibia, 3.6; metatarsus,

Figures 101–109. *Wixia georgia* n. sp. 101–104. Epigynum. 101. Ventral. 102. Posterior. 103. Lateral. 104. Posterior, cleared. 105. Female. 106. Female abdomen, posterior. 107. Female, lateral. 108–109. Male left palpus. 108. Mesal. 109. Ventral.

Figures 110–112. *Wixia*, male second left patella and tibia. 110. *W. ectypa*, anterior. 111. *W. georgia*, posterior. 112. *W. globosa*, posterior.

Scale lines. 0.1 mm, except Figs. 105–107, 110–112, 1 mm.

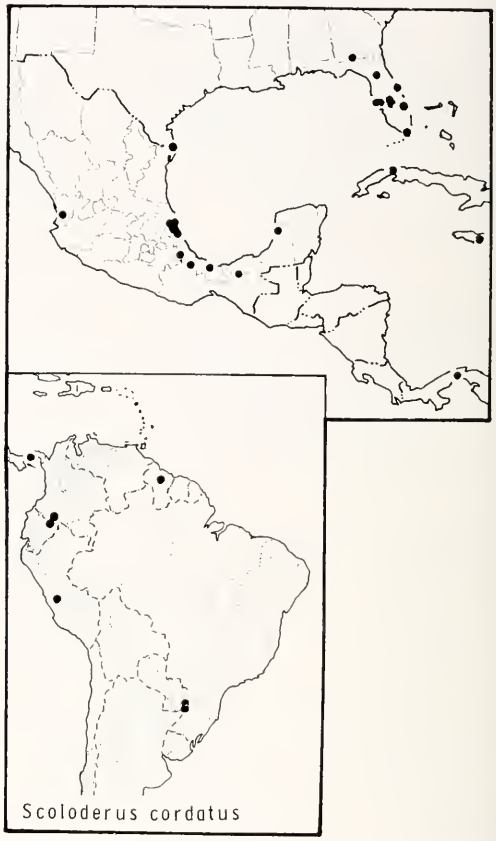
1.9; tarsus, 0.8. Second patella and tibia, 2.7 mm; third, 1.9; fourth, 2.9.

Variation. Females vary in total length 3.7 to 6.3 mm, carapace 2.5 to 3.2 long, 2.2 to 2.4 wide.

Diagnosis. The transverse groove behind the posterior lip of the epigynum separates females from *W. georgia* (Figs. 117–118). The transverse groove is much shallower than the one of *W. subrufa* F. P.-Cambridge of Guatemala. The shape of the terminal apophysis and embolus (Figs. 115, 121) separates males from *W. georgia.*

Natural history. Mature females have been found from August to October, a mature male was collected in October. There are no habitat observations.

Distribution. Kansas, Arizona south to southern Mexico (Map 5).



Map 6. Distribution of *Scoloderus cordatus* (Taczanowski).

Scoloderus Simon

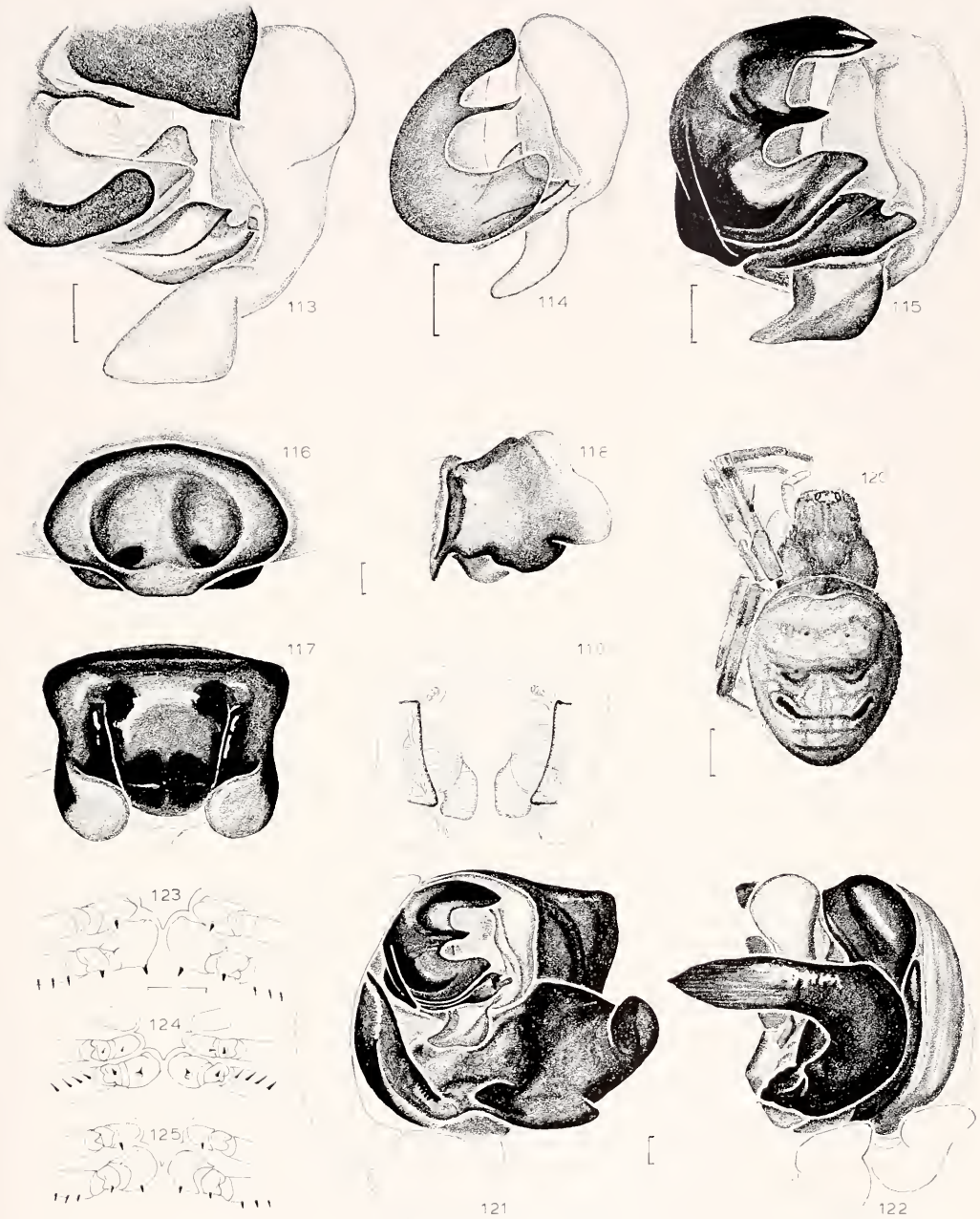
Scoloderus Simon, 1887, Ann. Soc. Entomol. France, ser. 6, 7: CLXXXVII. Type species by original designation *Hypophthalma cordata* Taczanowski. The name is masculine.

Diagnosis. Scoloderus is close to *Wixia* but differs in the high, bulging carapace (Figs. 126, 127), and from many other genera in the high abdomen attached to the cephalothorax at an angle (Fig. 127). Unlike *Mangora,* which has the abdomen similarly attached, *Scoloderus* has no trichobothria anteriorly on the third tibia.

Genitalia. The epigynum is a plate with a posterior lobe (Fig. 129) and openings on the posterior face (Fig. 130); a blind internal sac perhaps has a coiled lumen (Fig. 131). The palpus has a conductor (c in Fig. 136), a large, broad median apophysis (m), and an embolus (e) with several lobes, one of which may be the terminal apophysis. *Scoloderus* lacks the paramedian apophysis seen in the related *Wixia.*

Description. Specimens of the two species differ greatly in degree of sclerotization and shape of abdomen. The carapace bulges in the thoracic region even in juveniles. The clypeus is about two times the diameter of the anterior median eyes (Fig. 126). The abdomen is attached at a right angle and is thus higher than long (Fig. 127). If weakly sclerotized the abdomen has dorsal humps (Fig. 128); if more heavily sclerotized, it is heart-shaped. The male is smaller than the female, its carapace as in the female, its abdomen almost lacking humps (Fig. 132). Palpul femur lacks basal tooth, patella has one weak macroseta. The first coxa has a hook on the distal margin, and the second tibia is swollen and has macrosetae (Fig. 133).

Species. There are two widespread similar American species, *S. cordatus* and *S. tuberculifer.* The genus is not known from other parts of the world. The numerous names in catalogs all refer to these two



Figures 113–115. *Wixia* embolus, terminal apophysis and conductor. 113. *W. ectypa.* 114. *W. georgia.* 115. *W. globosa.*

Figures 116–122. *Wixia globosa* F.P.-Cambridge. 116–119. Epigynum. 116. Ventral. 117. Posterior. 118. Lateral. 119. Posterior, cleared. 120. Female. 121, 122. Left male palpus. 121. Mesal. 122. Ventral.

Figures 123–125. *Wixia*, fourth coxa and trochanter. 123. *W. ectypa.* 124. *W. georgia.* 125. *W. globosa.*

Scale lines. 0.1 mm except Fig. 120, 1 mm.

species. The variable shape of the abdomen and degree of sclerotization has led describers astray.

Scoloderus cordatus (Taczanowski)
Plate 6, Figures 126–136, Map 6

Hypophthalma ? cordata Taczanowski, 1879, Horae Soc. Entomol. Rossicae, 15: 129, pl. 2, fig. 40, ♀. Female lectotype here designated, from Amable María [Tarma Prov., Dept. Junín], Peru in the Polish Academy of Sciences, examined.

Hypophthalma ? cresimorpha Taczanowski, 1879, Horae Soc. Entomol. Rossicae, 15: 130, pl. 2, fig. 41, ♂. Juvenile male holotype from Amable María [Tarma Prov., Dept. Junín], Peru, in the Polish Academy of Sciences, examined. NEW SYNONYMY.

Scoloderus cordatus, – Simon, 1887, Ann. Soc. Entomol. France, ser., 6, 7: CLXXXVII.

Carepalxis tuberculifer, – McCook, 1893, American Spiders, 3: 207, pl. 3, fig. 6, ♀. Not *S. tuberculifer.*

Carepalxis nigriceps O. P.-Cambridge, 1895, Biologia Centrali-Americana, Araneidea, 1: 158, pl. 19, fig. 9, ♀. Female holotype from Teapa, Mexico in the British Museum, Natural History, examined. NEW SYNONYMY.

Scoloderus gibber O. P.-Cambridge, 1898, Biologia Centrali-Americana, 1: 282, pl. 36, fig. 4, ♀. Female holotype from Atoyac, Veracruz, Mexico in the British Museum, Natural History, examined. F. P.-Cambridge, 1904, op. cit., 2: 521, pl. 51, fig. 8, ♀. Roewer, 1942, Katalog der Araneae, 1: 872. NEW SYNONYMY.

Scoloderus nigriceps, – F. P.-Cambridge, 1904, Biologia Centrali-Americana, Araneidea, 2: 521, pl. 51, fig. 7, ♀.

Scoloderus tuberculifer, – Comstock, 1912, Spider Book, p. 447, fig. 456, ♀. Comstock, 1940, Spider Book, rev. ed., p. 461, fig. 456, ♀. Not *S. tuberculifer* (O. P.-Cambridge).

Scoloderus birabeni Mello-Leitão, 1945, Rev. Mus. La Plata, nueva serie, secc. zool., 4: 242. Female holotype from Puerto Victoria, Misiones Province, Argentina in the Museum of La Plata, examined. NEW SYNONYMY.

Scoloderus intermedius Pikelin and Schiapelli, 1948, Comun. Mus. Argentino Cienc. Natur., ser. zool., 4: 13, figs. 14–17, ♀. Female holotype from Santa María, Misiones Province, Argentina in the Museo Argentino de Ciencias Naturales. NEW SYNONYMY.

Note. Specimens in collections have been labeled *Wixia* sp., *Wixia ectypa*, some as *Scoloderus* sp. and *Scoloderus tuberculifer.*

Description of female from Florida. Carapace dark brown with paired black patches on anterior slope. Chelicerae brown, darker distally. Sternum brown, coxae light brown. Legs brown, distal articles lighter. Dorsum of abdomen whitish, sometimes with transverse black bars. Center of venter without pigment. Posterior median eyes 1.3 diameters of anterior medians, laterals 0.8; anterior medians 1.4 diameters apart, posterior medians 1.5. The anterior margin of the chelicerae has four teeth, the third from distal end largest; posterior margin has three teeth, the third from distal end largest. Total length 3.7 mm. Carapace 1.5 mm long, 1.3 wide. First femur, 1.9 mm; patella and tibia, 1.8; metatarsus, 0.9; tarsus, 0.4. Second patella and tibia, 1.5 mm; third, 1.0; fourth, 1.2.

Male. Much darker than female, thoracic area and sides darker and more dark marks on posterior of abdomen. Anterior median eyes slightly larger than in female, separated by about same distances. Total length 2.4 mm. Carapace 1.3 mm long, 1.2 wide First femur, 1.7 mm; patella and tibia, 1.7; metatarsus, 0.9; tarsus, 0.5. Second patella and tibia, 1.3 mm; third, 0.8; fourth, 1.0.

Variation. Abdomen usually has two dorsal humps and one smaller median hump more anterior. Humps rarely subdivided. Abdomen variable in shape and in some more sclerotized South American specimens, abdomen lacks humps and is shield-shaped. Females north of Mexico vary in total length from 3.2 to 4.3 mm, carapace 1.5 to 2.0 long, 1.3 to 1.7 wide. Males, total length 2.3 to 2.8 mm, carapace 1.4 to 1.5 long, 1.2 to 1.4 wide.

Diagnosis. The epigynum of *S. cordatus* has a semicircular posterior lobe (Fig. 129); that of *S. tuberculifer* has a narrow lobe with parallel sides. In cleared preparations the connecting duct of *S. cordatus* appears straight (Fig. 131), that of *S. tuberculifer* has a posterior loop. The palpus of *S. cordatus* has a median apophysis with a narrow distal rim (Fig. 135); in *S. tuberculifer* the rim is half the

Figures 126–136. *Scoloderus cordatus* (Taczanowski). 126–131. Female. 126. Eye region and chelicerae. 127. Lateral. 128. Dorsal. 129–131. Epigynum. 129. Ventral. 130. Posterior. 131. Posterior, cleared. 132–136. Male. 132. Dorsal. 133. Left second leg, anterior. 134. Abdomen, dorsal. 135. Left palpus, mesal. 136. Palpus, expanded.

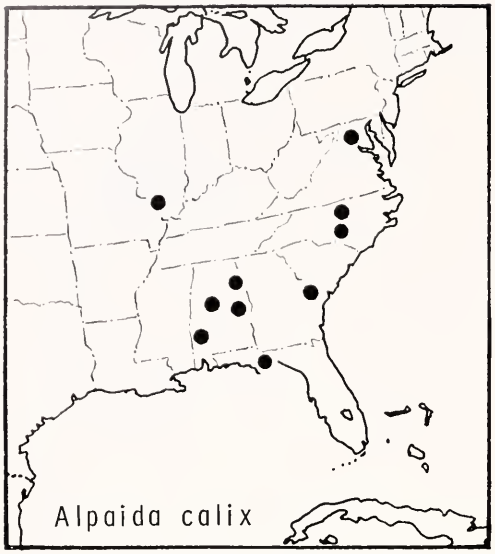
Abbreviations. c, conductor; e, embolus; m, median apophysis; r, radix; t, tegulum.

Scale lines. 0.1 mm, except Figs. 126–128, 132–133, 1.0 mm.

length of the median apophysis. In the two species the sclerites around the embolus differ in shape.

Natural history. Females have been collected in woods all year, males in March, April, September and December in Florida. Only the web of *S. tuberculifer* is known, first found by W. Eberhard in Colombia[1]

[1] See also W. G. Eberhard, 1975, J. Natur. Hist., **9**: 93–106. Mark Stowe found the web of *S. cordatus* in Florida on palmettoes in July 1975. It was 40 cm long.



Map 7. Distribution of *Alpaida calix* (Walckenaer).

(Plate 6). It is unique, a similar but upside-down version of the web illustrated by Robinson (1972) of an unknown New Guinea Metinae.

Distribution. From southern Georgia to Texas, south to northern Argentina (Map 6).

Alpaida O.P.-Cambridge

Alpaida O. P.-Cambridge, 1889, Biologia Centrali-Americana, Araneidea, 1: 52. Type species by monotypy *A. conica*. The name is feminine.

Parepeira Mello-Leitão, 1933, Arch. Escuela Sup. Agric. Med. Veter., 10(1): 3–63 (not seen). Type species *Epeira albostriata* Keyserling. NEW SYNONYMY.

Subaraneus di Caporiacco, 1945, Proc. Zool. Soc. London, 118: 661. Type species by original designation *Epeira veniliae* Keyserling. NEW SYNONYMY.

Lariniacantha Archer, 1951, Amer. Mus. Novitates, no. 1487: 15. Type species *Epeira grayii* Blackwall, 1863 by original designation. NEW SYNONYMY.

Subedricus di Caporiacco, 1954, Comment. Pontificia Acad. Scient., 16: 84. Type species *Epeira nigropostulatus* O. P.-Cambridge by original designation. NEW SYNONYMY.

Note. This genus includes the majority of South and Central American species described in *Epeira, Aranea, Araneus* and *Singa*. Mello-Leitão placed species belonging to this genus in *Wixia* in the 1940's, Archer in *Lariniacantha*.

Diagnosis. Alpaida differs from *Araneus* and *Singa* by the genitalia. The epigynum is a broad lobe without a scape (Figs. 140, 141). Unlike the palpi of *Singa* and *Hypsosinga*, the palpus in *Alpaida* has the tegulum lateral, the sclerites facing mesally (Fig. 143). There is a terminal apophysis (a in Fig. 144), generally with two, usually heavily sclerotized lobes, one of which may be the subterminal apophysis. The median apophysis (m) is bulky, variously shaped, and also heavily sclerotized. *Alpaida* lacks the paramedian apophysis seen in *Eriophora, Verrucosa* and *Wixia*. Species are most easily assigned to the genus on the bases of the characteristic epigynum and the shape and color of the abdomen.

Coloration. Carapace, sternum yellow-white to brown. Legs usually not banded. Eyes often on black spots. The abdomen is often brightly marked, frequently with longitudinal bands.

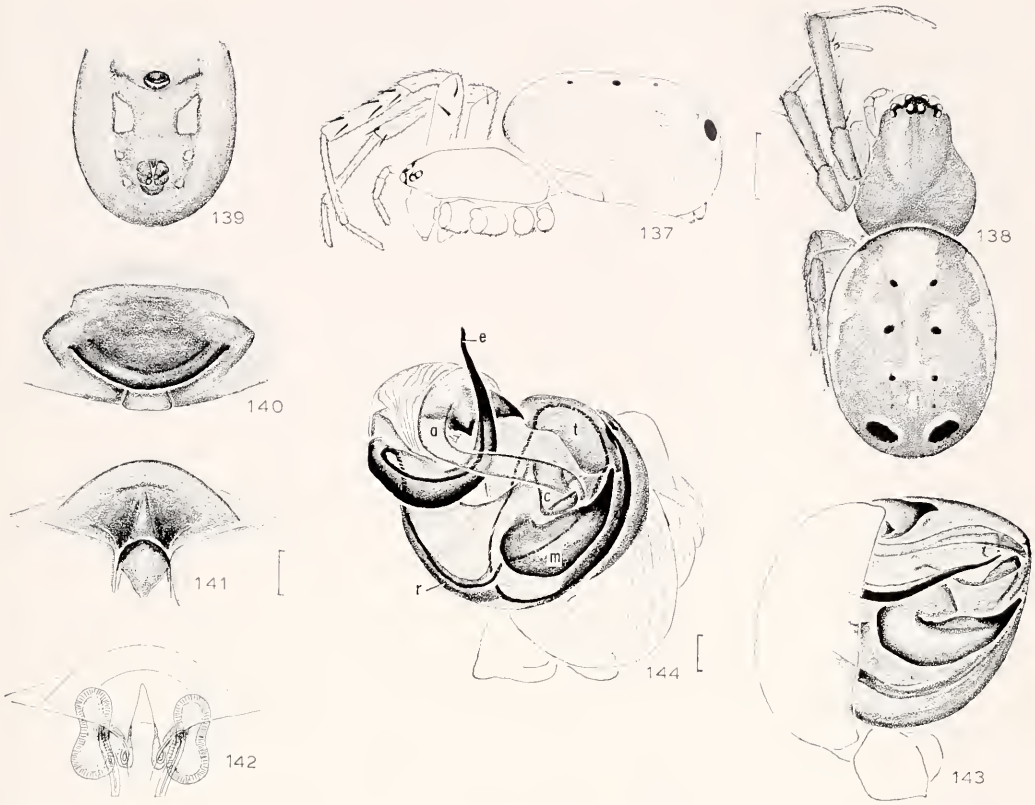
Structure. The carapace is smooth, without setae, wider than eyes in eye region of female. The lateral eyes are distant from the medians. The abdomen generally is shield-shaped, usually widest anteriorly; sometimes widest posteriorly and truncate. There may be sclerotized spines at the anterior end of the abdomen; sometimes the muscle scars are sclerotized, but there are few setae.

Species. Alpaida is known only from tropical America; a few species, including *A. calix*, extend into the temperate zone. There may be 50 to 100 species. *Alpaida calix* is not a characteristic member of the genus, its placement is in doubt and may eventually have to be changed.

Alpaida calix (Walckenaer), new combination

Figures 137–144, Map 7

Epeira calix Walckenaer, 1841, Histoire Naturelle Insectes Aptères, 2: 90. The types are Abbot manuscript illustrations, no. 249, 250 from Georgia in the British Museum, Natural History;



Figures 137–144. *Alpaida calix* (Walckenaer). 137–142. Female. 137. Lateral. 138. Dorsal. 139. Abdomen, ventral. 140–142. Epigynum. 140. Ventral. 141. Posterior. 142. Posterior, cleared. 143–144. Left male palpus. 143. Mesal. 144. Expanded, submesal.

Abbreviations. a, terminal apophysis; c, conductor; e, embolus; m, median apophysis; r, radix; t, tegulum.

Scale lines. 0.1 mm, except Figs. 137–139, 1.0 mm.

Copies of the manuscript in the Museum of Comparative Zoology, examined.

Epeira maura Hentz, 1847, J. Boston Soc. Natur. Hist., 5: 474, pl. 31, fig. 8, ♀. Female holotype from Alabama in the Boston Natural History Society, destroyed.

Singa maura, – Keyserling, 1884, Verhandl. Zool. Bot. Gesell. Wien, 34: 527, pl. 13, fig. 26, ♀. Keyserling, 1893, Spinnen Amerikas, 4: 283, pl. 14, fig. 208, ♀. McCook, 1893, American Spiders, 3: 234, pl. 19, fig. 8, ♀. Roewer, 1942, Katalog der Araneae, 1: 878.

Leucauge maura, – F. P.-Cambridge, 1903, Biologia Centrali-Americana, Araneidea, 2: 443.

Araneus maurus, – Bonnet, 1955, Bibliographia Araneorum. 2: 542.

Note. The name *maura* was first synonymized with *calix* by Chamberlin and Ivie (1944).

Description. Female. Carapace, sternum and legs orange-brown, eye area blackish. Abdomen has dorsal white marks, two black spots posteriorly surrounded by white (Fig. 138). The venter has two white longitudinal marks on each side of median dark area. Anterior median eyes largest, secondary eyes 0.8 diameter of anterior medians. Anterior median eyes one diameter apart, one diameter from laterals. Posterior medians their radius apart, two diameters from laterals. The height of the clypeus is less than the radius of the anterior median eyes. The anterior margin of the chelicerae has four teeth, the posterior row three. Legs are strong, short,

with few macrosetae. Abdomen is oval. Total length 6 mm. Carapace 2.3 mm long, 1.8 wide. First femur, 2.0 mm; patella and tibia, 2.5; metatarsus, 1.5; tarsus, 0.8. Second patella and tibia, 2.2 mm; third, 1.2; fourth, 1.7.

Male. Coloration like that of female, but white marks on dorsum less distinct. Carapace is narrower, a slight thoracic depression with a longitudinal line. Secondary eyes are equal to the radius of the anterior median eyes. Eye spacing as in female. The first coxa has a hook on distal margin, the first and second legs have many macrosetae, but are not otherwise modified. Total length 4.0 mm. Carapace 2.3 long, 1.8 wide. First femur, 2.0 mm; patella and tibia, 2.6; metatarsus, 2.0; tarsus, 0.9. Second patella and tibia, 2.3 mm; third, 1.3; fourth, 2.0.

Variation. This species is thought to be deep crimson or sepia except for the light patches when alive. Total length of female is 3.9 to 6 mm, carapace width 1.6 to 1.9. Total length of males is 3.8 to 4.0 mm, carapace width 1.7 to 1.8.

Diagnosis. The oval abdomen with two posterior spots (Fig. 138) separates *A. calix* from other *Alpaida*. Unlike other *Alpaida* the abdomen is oval rather than elongate and the eyes are spaced more closely. There is a slight doubt on the placement of this species. Perhaps the species belongs to *Bertrana* or another *Alpaida* related genus.

Natural history. Alpaida calix has been collected by sweeping bottomland pine and hardwood and in hardwood forest in North Carolina. Males seem to be mature in spring, females until September.

Distribution. From Washington, D.C. and southern Illinois to Alabama and northern Florida (Map 7).

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The Nearctic Hahniidae (Arachnida: Araneae)

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THE NEARCTIC HAHNIIDAE (ARACHNIDA: ARANEAE)[1]

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ABSTRACT. The taxonomy of the North American and Mexican members of the family Hahniidae is revised; two genera and five species are placed in synonymy, eight new species are described and illustrated, and 20 species are redescribed, illustrated, and their distributions updated. Observations on the biology of some of these small, ecribellate, entelegyne spiders are included.

INTRODUCTION

The family Hahniidae includes small entelegyne, ecribellate spiders of the suborder Labidognatha. They can be recognized by the transverse arrangement of three pairs of spinnerets and by the location of a single broad spiracle much in advance of the spinneret bases (Figs. 1, 4, 10, 11). Their eight eyes are arranged in two slightly procurved rows (Figs. 3, 9, 12). The tarsus of each leg bears three serrate claws without claw tufts. The ovate abdomen of the hahniids is brown and in many specimens has several light dorsal chevrons set off by gray markings. The legs may be either unicolored or banded (Plate 2, Fig. 2).

Hahniidae have a world-wide distribution, and are represented in the Nearctic by three genera and 28 known species, in the Neotropic by seven genera and 14 known species, in the Palearctic by five genera and 21 known species, in the Orient by four genera and nine known species, in the Australian zone by ten genera and 33 known species, and in the Ethiopian zone by three genera and ten known species. Three of the Nearctic species are widely distributed. The remainder have a more restricted range.

The Hahniidae of America north of Mexico were treated by Gertsch (1934), who, as did other authors, later described additional species of the family. In the last several years many new collections have become available, making a more thorough revision of the group possible.

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POSITION OF THE FAMILY

Since Bertkau (1878) erected the family Hahniidae using *Hahnia* C. L. Koch as the type genus it has been treated as both a family (Petrunkevitch, 1933; Gerhardt and Kaestner, 1938; Kaston, 1948) and as a subfamily of the Agelenidae (Emerton, 1890, Simon, 1892; Bristowe, 1938; Gertsch, 1949; Bonnet, 1959; Kaestner, 1968). Gerhardt and Kaestner and Kaston place the family Hahniidae in the superfamily Lycosoidea. The members of this superfamily have tracheae which extend into the cephalothorax. Agelenidae, Pisauridae, Lycosidae, and Oxyopidae have three pairs of cardiac ostia while the other members of this superfamily, Argyronetidae, Senoculidae, and Hahniidae, have two pairs of cardiac ostia (Petrunkevitch, 1933).

Lehtinen (1967) proposes quite a different classification which reclassifies the agelenid tribe Cryphoeceae of the subfamily Ageleninae (Simon, 1897) and part of the agelenid subfamily Cybaeinae (Petrunkevitch, 1928) as the subfamilies Cryphoecinae and Cybaeolinae, respectively, of the family Hahniidae. Lehtinen groups the Hahniidae with the Miturgidae, Amaurobiidae, Lioeranidae, Agelenidae, and Dictynidae in the superfamily Amaurobioidea which is part of the Amaurobiides-group of the suborder Araneomorpha. Although the Cryphoecinae and Cybaeolinae resemble the Hahniidae more closely than do other Agelenidae, the more widely accepted definition of the family Hahniidae clearly excludes these two agelenid groups. We have followed this definition here.

The classification proposed by Forster (1970) supports in principle that of Lehtinen (1967), but follows the more widely accepted definition of the Hahniidae. This family, along with the Dictynidae, Desidae, Cybaeidae, Argyronetidae, and Anyphaenidae, is placed in the araneomorph superfamily Dictynoidea. Dictynoidea includes families, members of which have strongly branched or divided median tracheae. Amaurobioidea, on the other hand, includes spider families with slender, unbranched tracheae.

The Hahniidae appear to be most closely related to the family Agelenidae, particularly of the subfamily Agelenidae group Cryphoeceae and the subfamily Cybaeinae. Both groupings contain small spiders found west of the Rocky Mountains in moist environments.

Two South American genera of the subfamily Ageleninae, *Lizarba* and *Mevianes*, resemble the genus *Hahnia* of the Hahniidae in general appearance and in certain features of the male and female genitalia, but differ from *Hahnia* in having a colulus, spinnerets which are not in a transverse row, and a spiracle near the base of the spinnerets.

Plate 1. Web of *Neoantistea agilis* (Keyserling) from Massachusetts. (From Ektachrome by H. W. Levi.)

NATURAL HISTORY OF THE HAHNIIDAE

Individuals of *Neoantistea* spin small sheet webs which are rarely more than two inches across and lack retreats. Webs are found in moist areas over small depressions in the soil or in moss (Plate 1), but are hard to see unless covered with dew. We have observed *N. agilis* on both the upper and lower surfaces of its web. When dis-

Plate 2. (Top) *Neoantistea agilis* (Keyserling) female from Massachusetts. (From Ektachrome by H. W. Levi.) (Bottom) Egg case produced by an *N. agilis* from Indiana (the space between vertical lines represents 1 mm).

turbed these spiders run quickly to the edge of the web and often take refuge in crevices of the soil, moss, or debris. So far as we know, no spiders of the genera *Antistea* or *Hahnia* have been seen on or taken from webs, although collecting data for many specimens do not mention habitat. Specimens of these two genera have been found under stones and wood, in leaves and litter, and in pitfall traps, as were many *Neoantistea*. Berry (1970) found *Hahnia* primarily in forest leaf litter. It may be that *Antistea* and *Hahnia* build small webs that have escaped notice. On the other hand, they may hunt small insects which are likely to be abundant where they have been found, and may not need webs.

The remains of prey have not been observed in the webs of *N. agilis* or *N. riparia*. Adult and subadult *N. agilis* are able to eat *Tribolium* larvae up to 7 mm in length. Upon hatching, *N. agilis* are less than one mm long and probably feed on Collembola and other small insects.

The egg sacs of Hahniidae are circular mounds covered by white silk (Plate 2). In the laboratory an *N. agilis* produced an egg sac which had a diameter of 4 mm and a height of 2 mm. After sixteen days, seven spiderlings, ranging in length from 0.84 to 0.96 mm, emerged from this sac. No unhatched eggs remained.

Collecting data for *H. cinerea*, *N. agilis*, *N. riparia*, and *N. magna* suggest that most reproduction occurs from late March to late May and again from mid-August to late September. Two peaks in adult and juvenile population are indicated, a smaller one during the latter two-thirds of April and a larger one from mid-August to mid-September. Most *N. agilis* immatures are taken during May and August while most *N. magna* immatures appear during April and July, indicating the reproductive isolation of these two sympatric species. The immature populations of *N. agilis* and *N. magna* are greatest during August and July, respectively.

Collecting records support the findings of Berry (1970) that *Neoantistea agilis*, *Hahnia cinerea*, and *H. flaviceps* are forest species, while *N. riparia* is found primarily in field environments. Although Berry found *N. magna* primarily in field environments, collecting records show that this species is common in the leaf litter of hardwood forests. *Antistea brunnea* and *H. glacialis* appear to be boreal species. *Neoantistea gosiuta* is found at elevations of 8,000 to 12,000 feet in forests of ponder-

osa pine, aspen, douglas fir, and lodgepole pine, as well as in meadows.

Petrunkevitch (1933) and Levi (1967) report a positive correlation between a more extensive tracheal system and a less developed circulatory system (as determined by the number of cardiac ostia). Petrunkevitch (1933) found spiders with a single broad tracheal spiracle in front of the spinnerets to have a highly developed tracheal system and hypothesized that this forward movement of the spiracle was associated with an increased reliance upon tracheal rather than lung respiration. Levi (1967) notes that to avoid excess water loss some small spiders have a heavily sclerotized exoskeleton or remain in moist habitats, and that they often have a spherical abdomen, even when other members of their genus are characterized by an elongate abdomen.

If an anteriorly placed spiracle is a valid criterion for judging tracheal system development, it may be that the *Neoantistea* are more advanced than either *Antistea* or *Hahnia*. *Neoantistea* webs constructed close to the ground or on vegetation help condense water as well as capture prey. This increased moisture may keep these spiders active during the hotter, dryer parts of the day.

METHODS

About 3,000 specimens were examined. When appropriate, epigyna were removed and cleared in clove oil. Measurements were made with an ocular micrometer installed in a binocular microscope. Specimens were placed in a Syracuse dish of ethanol with a layer of fine, white sand. This allowed measurement of each structure in as nearly a horizontal plane as possible. Total lengths and, in larger specimens, dimensions of cephalothorax and abdomen were measured under 30–60× magnification, while other measurements were made under 75–90× magnification. Micrometer units were converted to metric units and these rounded to the nearest 0.01 mm.

DESCRIPTIONS

The generic descriptions give a more comprehensive account of coloration and morphology, while species descriptions include features not common to all members of the genus and those helpful in identification of species. Only 15 of the 53 measurements taken proved useful in species identification. Some of these are included in the description of each species and others can be found in Opell (1974). Unless otherwise indicated, measurements are of both males and females.

DISTRIBUTION

Maps and distribution records are based solely on specimens examined by the authors. Opell (1974) gives a complete list of most localities for all species except *Neoantistea inaffecta*, *N. oklahomensis*, *N. spica*, *N. unifistula*, and *Hahnia nobilis*.

HAHNIIDAE

Hahniidae Bertkau, 1878, Arch. Natur., 44: 351–410. Type genus by monotypy: *Hahnia* C. L. Koch.

Description. Hahniidae have diaxial chelicerae, two book lungs, a single, broad, median spiracle located in advance of the spinneret bases (Figs. 1, 4, 10, 11), tracheae which extend into the cephalothorax, two pairs of cardiac ostia, three pairs of spinnerets arranged in a transverse row (Figs. 1, 4, 10, 11), no cribellum or calamistrum, eight eyes arranged in two slightly procurved rows (Figs. 3, 9, 12), three serrate tarsal claws without claw tufts on each leg, a low, cone-shaped anal tubercle, and endocephalic poison glands.

The median pair of spinnerets of hahniida corresponds to the posterior median spinnerets of other spiders, the intermediate pair to the anterior median spinnerets of other spiders, and the lateral pair to the posterior lateral spinnerets of

other spiders (Marples, 1967). The median spinnerets are unsegmented, but both the intermediate and lateral pairs have two segments. The distal segment of the intermediate spinnerets is less than one-fourth the length of the proximal segment. In *Antistea* and *Neoantistea* the distal segment of the lateral spinnerets is as long as or longer than the proximal segment (Figs. 1, 4), while in *Hahnia* the distal segment is about one-half as long as the proximal segment (Figs. 10, 11).

In *Antistea* the spiracle is situated midway between the epigastric furrow and the base of the median spinnerets (Fig. 4), in *Hahnia* it is nearer the spinnerets (Figs. 10, 11), and in *Neoantistea* it is nearer the epigastric furrow (Fig. 1).

Petrunkevitch (1933) found that in *Neoantistea agilis* the spiracle led to a shallow atrium with two stout trunks that continued through the petiole into the cephalothorax, giving off tubules to supply the abdomen. In the cephalothorax the two trunks split into hundreds of tubules branching off to every appendage. Forster (1970) reported a somewhat different arrangement in a *N. agilis* specimen from Massachusetts. The broad spiracle led to two short lateral trunks which opened into a common atrium from which two median and two lateral lobes arose. The two median lobes were joined by a duct and from the distal portion of each of these four lobes a bundle of tracheae extended through the petiole and a few passed posteriorly into the abdomen.

In females the two epigynal openings are slits or narrow ovals found in the anterior (Fig. 20), median (Fig. 38), or posterior (Fig. 84) region of the epigynum. From each opening, flattened bursae, which may be either long (Fig. 55) or short (Fig. 21), generally lead to various-sized bulbs. In some species bulbs are absent and the bursae connect directly to ducts (Figs. 67, 107). Ducts connecting bulbs and spermathecae may be either short and simple (Figs. 65, 84) or long and convoluted (Figs. 6, 15). A thin fertilization duct leads from each spermatheca dorsally into the abdomen.

A Key to the Genera of Hahniidae

1 Spiracle equidistant from epigastric furrow and base of spinnerets or nearer to epigastric furrow (Figs. 1, 4). Anterior median eyes (AME) nearly as large as to larger than anterior lateral eyes (ALE) (Figs. 3, 9) with a stridulatory organ consisting of a file dorso-lateral to the petiole and a series of picks on posterior carapace. 2

– Spiracle nearer to base of spinnerets than to epigastric furrow (Figs. 10, 11). AME considerably smaller than ALE (Fig. 12) without a stridulatory organ as above. ..... *Hahnia*

2(1) Spiracle equidistant between epigastric furrow and base of spinnerets (Fig. 4). Median spinnerets separated by one-half their diameter or less at their bases. Proximal segment of lateral spinnerets longer than distal segment ..... *Antistea*

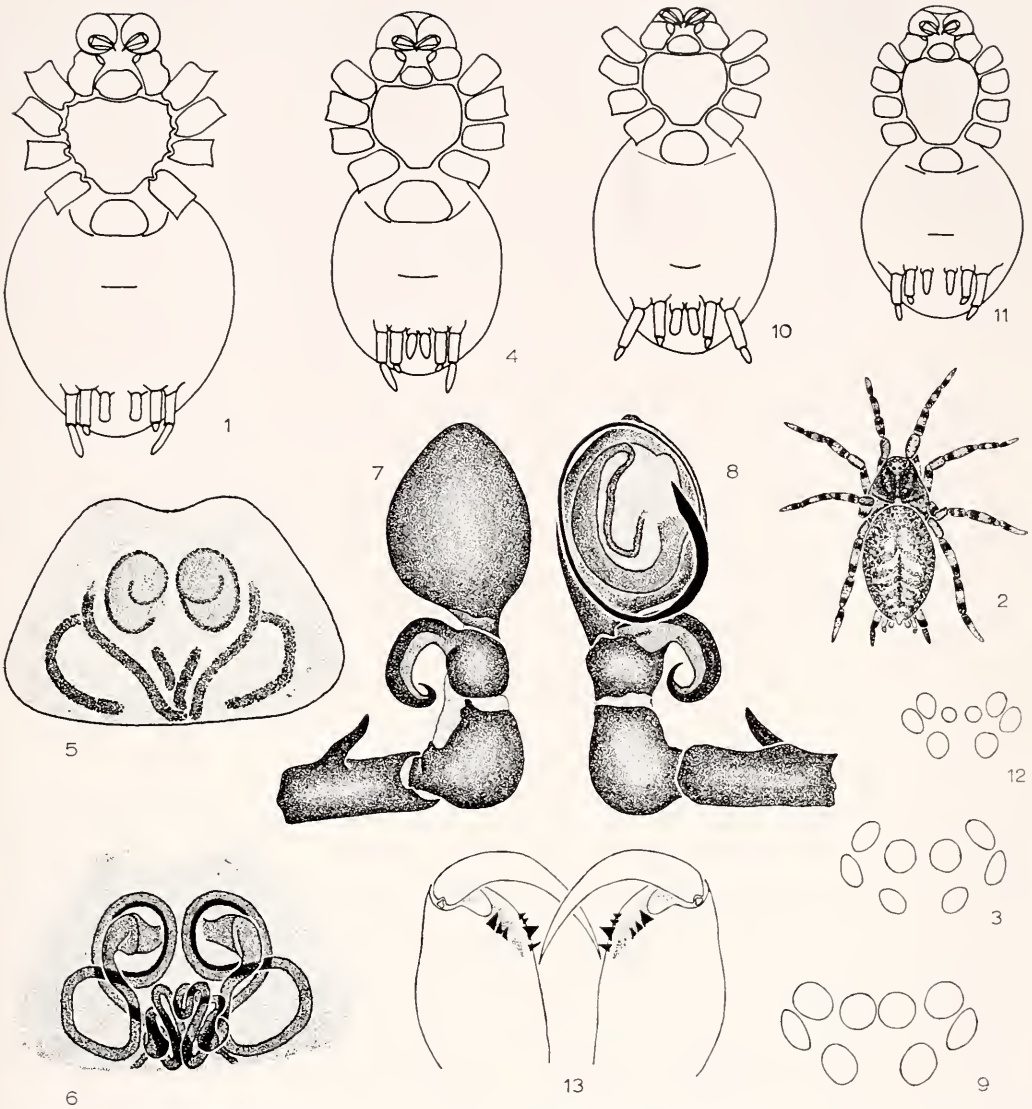
– Spiracle twice as far from base of spinnerets as from epigastric furrow (Fig. 1). Median spinnerets at least one diameter apart at bases. Proximal and distal segments of lateral spinnerets nearly equal in length. ..... *Neoantistea*

Antistea

Antistea Simon, 1898, Histoire Naturelle des Araignées, 2(2): 275. Type species by monotypy: *Agelena elegans* Blackwall, 1841, Tran. Linn. Soc. London, 18: 619, from England. The genus name is feminine.

Diagnosis. *Antistea* differs from *Neoantistea* and *Hahnia* by having the spiracle situated midway between the epigastric furrow and the base of the median spinnerets (Fig. 4), by having the proximal segment of the lateral spinnerets longer than the distal segment, and by having AME and PME nearly equal in diameter (Fig. 9). A stridulatory file is formed by two patches of appressed setae lying dorsal and lateral to the petiole. A series of short, stout setae on the carapace's posterior surface forms a pick.

Discussion. This genus contains only the European species, *Antistea elegans* Blackwall, and the North American species, *Antistea brunnea* (Emerton). The nearly equal



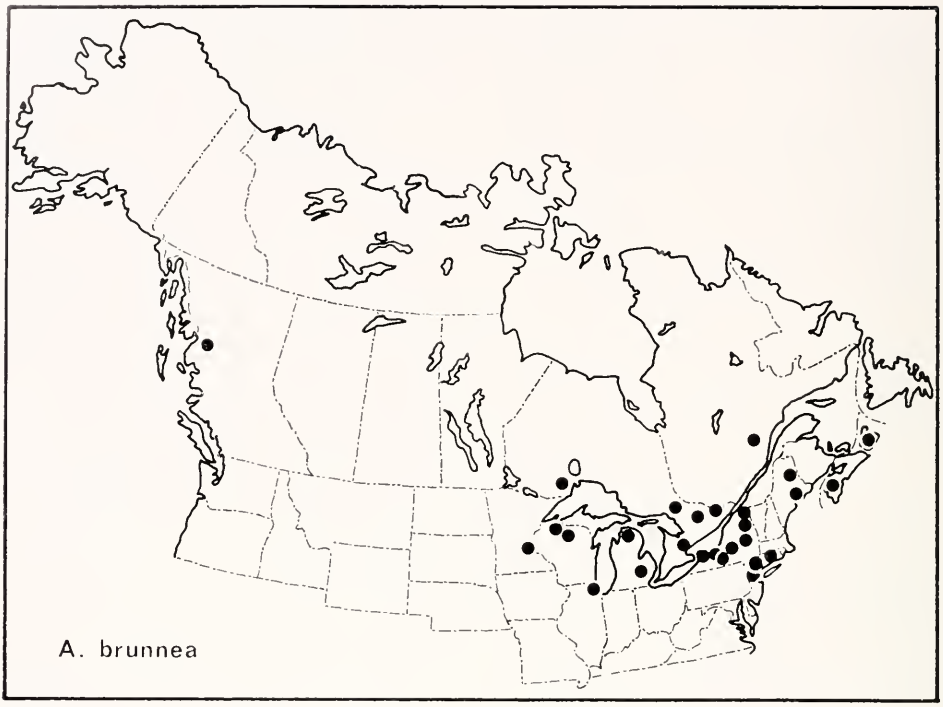
Figures 1–3. *Neoantistea agilis* (Keyserling). 1. Ventral view of female. 2. Dorsal view of female. 3. Dorsal view of ocular area.

Figures 4–9. *Antistea brunnea* (Emerton). 4. Ventral view of female. 5. Ventral view of epigynum. 6. Dorsal view of cleared epigynum. 7. Dorsal view of left male palpus. 8. Ventral view of left male palpus. 9. Dorsal view of ocular area.

Figure 10. Ventral view of *Hahnia sanjuanensis* Exline female.

Figures 11–12. *Hahnia cinerea* Emerton. 11. Ventral view of female. 12. Dorsal view of ocular area.

Figure 13. Ventral view of chelicerae of *Neoantistea magna* (Keyserling) female.



Map 1. Distribution of *Antistea brunnea* (Emerton).

size of the AME and PME, the anterior position of the spiracle, and the stridulatory organ indicate that *Antistea* may be more closely related to *Neoantistea* than to *Hahnia*. Although Lehtinen (1967) suggests that *Hahnia flaviceps* Emerton is closely related to the genus *Antistea*, the characteristics of this species identify it as a member of the genus *Hahnia*, a genus showing much more diversity than the *Antistea*.

Antistea brunnea (Emerton)
Figures 4–9; Map 1

Hahnia brunnea Emerton, 1909, Trans. Connecticut Acad. Arts Sci., 14: 223–224, pl. 8, fig. 5, ♀. Female holotype from Clarendon Hills maple swamp, Hanover, Grafton Co., New Hampshire, in Museum of Comparative Zoology, examined.

Antistea brunnea, – Gertsch, 1934, Amer. Mus. Novitates, No. 712: 15, figs. 31–33, ♂, ♀.

Description. Carapace brown with darker cervical grooves, thoracic groove, and radial furrows. Dorsum of abdomen dark brown or gray with six light chevrons, each divided by a median gray line. Legs, palps, and spinnerets brown. Total length 2.20 to 5.10 mm. Carapace about 1.12 mm long, 1.00 wide. Eye ratio AME:ALE:PME:PLE = 1:1.2:1:1. Sternum length and width about 0.65 mm. Labium 0.14 mm long, 0.22 mm wide. Each chelicera with two to four retromarginal teeth, three being the usual number. Abdomen 1.43 to 2.02 mm long. Distance from spiracle to spinnerets 0.94 times the distance from spiracle to epigastric furrow. Proximal segment of the lateral spinnerets 1.45 times as long as distal segment.

Diagnosis. Male palpus with a tibial apophysis which is retrolateral, distal, broad, tapered to a point, and makes one complete dorsal spiral (Figs. 7, 8). Patella globose with no spur. Femur with a bent,

median, retrolateral apophysis which is about as long as femur is wide and is directed distally to form a 50° angle with the femur. Cymbium oval, broader than long. Epigynal openings of female are in the center of a spiral formed by the ducts and connect by short bursae to the median, ventral surfaces of the laterally-compressed bulbs which are about the same size as the spermatheeae (Figs. 5, 6). The ducts make two loops, one lateral and one anterior, and at the posterior, median area of the epigynum are more convoluted and asymmetrical.

Discussion. *Antistea brunnea* is similar to the European species *Antistea elegans*, but details of the genitalia separate these species. The patellar spur of *A. brunnea* is flattened and forms a spiral (Fig. 7) while that of *A. elegans* is flattened, recurved, and twisted. The patellar spur of *A. elegans* bends more deeply. Differences in female genitalia (small variations in duct coils) are less striking.

Distribution. Nova Scotia south to northern New Jersey and northern Illinois, west to central Minnesota and western central British Columbia (Map 1).

Neoantistea Gertsch

Neoantistea Gertsch, 1934, Amer. Mus. Novitates, No. 712: 2, 18–19. Type species, by original designation, *Hahnia agilis* Keyserling, 1887, Verh. Zool. Bot. Ges. Wien, 37: 465–467. The genus name is feminine.

Diagnosis. Characteristic features of the genus *Neoantistea* include a spiracle twice as far from the base of the median spinnerets as from the epigastric furrow (Fig. 1), proximal and distal segments of the lateral spinnerets nearly equal in length, and AME nearly as large as or larger than PME (Fig. 3). A stridulatory file is formed by two patches of appressed setae lying dorsal and lateral to the petiole. The pick is formed by a series of short, stout setae on the carapace's posterior surface.

Discussion. Eighteen species of *Neoantistea* occur in the Nearctic. Although Gertsch (1934) described this genus as being "strictly Nearctic," the collection of *N. lyrica* from Costa Rica establishes a Neotropic distribution for the genus. Species level identification of *Neoantistea* specimens, especially the males, is sometimes difficult. You must clear the epigynum to accurately use the key to the females. The number of retromarginal teeth on each chelicera is a character several places in the keys and in the species descriptions. Do not rely on this character alone, since the number of teeth may not always be constant for a given species, and the viewing angle may hide the separation between adjacent teeth.

Coloration. Carapace reddish brown and shiny; margin, cervical grooves, thoracic groove, and radial furrows usually darker (Plate 2, Fig. 2). Chelicerae, endites and labium brown. Sternum reddish brown, margin sometimes dusted with gray. Legs usually banded; femur, tibia, and metatarsus each with proximal and distal gray rings; tarsus with only proximal gray ring; patella with gray lateral margins. Legs of *N. hidalgoensis*, *N. lyrica*, *N. pueblensis* and *N. unifistula* without bands. Dorsum and lateral surfaces of abdomen tan, mottled with gray. Anterior one-third to one-half of dorsum with two reddish muscle attachments, often within a light oval. Posterior portion of dorsum with two to six (five or six in most) light, anteriorly-directed chevrons; the anterior ones bisected by a median gray line. Lateral surfaces of abdomen with gray dots often arranged in oblique rows. Venter of abdomen tan with no prominent markings. Anterior and median spinnerets tan, lateral spinnerets tan with distal gray ring on proximal segment and gray dorsum on the distal segment.

Structure. Total body length ranges from 2.30 to 4.76 mm of which the abdomen comprises about two-thirds. Carapace slightly longer than wide, cephalic region about two-thirds as wide and twice as high as thoracic region. Posterior eye row more

strongly procurved than anterior eye row. Median ocular quadrangle narrows anteriorly. AME of most species about 1.5 times the diameter of the PME (Fig. 3). In *N. hidalgoensis*, *N. jacalana*, *N. inaffecta*, *N. pueblensis*, *N. spica*, and *N. unifistula* the PME is as large as or slightly larger than AME. Each chelicera with one to four retromarginal teeth (Fig. 13). Endites equal in length and width (Fig. 1). Labium and sternum each slightly wider than long. Leg length commonly IV, I, II, III. Distance from spiracle to spinnerets 1.8–3.3 times the distance from spiracle to epigastric furrow. Proximal segments of lateral spinnerets 0.9 to 1.4 times longer than distal segments.

Male palpus with femur and tarsus about equal in length (Figs. 18, 19), each nearly equal to the combined lengths of patella and tibia. Tibial apophysis located distally and retrolaterally and, when curved, directed proximally. Patellar spur (present in all but *N. lyrica*) located proximally and retrolaterally and, when curved, directed distally. Cymbium oval, slightly longer than wide. Seminal canal encircles distal and lateral two-thirds of bulbal apparatus, decreasing in width and forming a prominent, oblique loop at the proximal, retrolateral area of the cymbium before joining the embolic region at the proximal prolateral region of the tarsus. The embolus originates near the base of the cymbium and curves around the periphery of the bulbal apparatus, making nearly a full turn. In *N. inaffecta* the embolus appears to lie in a groove at the base of the tibial apophysis (Figs. 68, 69). The epigyna of all species except *N. unifistula* (Figs. 76, 77) have openings which are anterior to the spermathecae (Fig. 64). Bulbs, found in the epigyna of all species but *N. inaffecta* (Fig. 67), are located anterior to the spermathecae and vary in size, being smaller than the spermathecae (Fig. 73), equal in size to the spermathecae (Fig. 65), or larger than the spermathecae (Fig. 77).

Key to Male *Neoantistea*

(Males of *N. jacalana*, *N. hidalgoensis*, *N. spica*, and *N. unifistula* are not known)

1 Patellar spur present (Fig. 18). 2
– Patellar spur absent (Figs. 50, 51). ..... *lyrica*
2(1) Basal two-thirds of tibial apophysis nearly perpendicular to long axis of tibia (Figs. 18, 36, 42, 58, 68, 74). 3
– Tibial apophysis curved strongly proximally (Figs. 24, 26, 30, 40, 46, 56, 62). 8
3(2) Patellar spur broad at base, conical or hooked at tip, about one-fourth as long as tibial apophysis (Figs. 36, 68, 74). 4
– Patellar spur slender and talonlike, about one-half to two-thirds as long as tibial apophysis (Figs. 18, 42, 58). 6
4(3) Tibial apophysis about as long as tibia is wide (Figs. 68, 74). 5
– Tibial apophysis about twice as long as tibia is wide (Figs. 36, 37). ..... *pueblensis*
5(4) Embolus encircles cymbium in the usual manner (Figs. 74, 75); one retromarginal tooth on each chelicera; Canada and the U. S. ..... *magna*
– Embolus lies in a groove at the base of the tibial apophysis (Figs. 68, 69); four retromarginal teeth on each chelicera; southwestern Mexico. ..... *inaffecta*
6(3) Patellar spur gradually curved to form an angle of about 45° with the long axis of the patella (Figs. 18, 19). ..... *agilis*
– Patellar spur abruptly bent so that the distal one-third is nearly parallel to the long axis of the patella (Figs. 42, 58). 7
7(6) From Oklahoma; three retromarginal teeth on each chelicera (Figs. 42, 43). ..... *oklahomensis*
– From Florida; one retromarginal tooth on each chelicera (Figs. 58, 59). ..... *alachua*
8(2) Tibial apophysis broad and dorsoventrally flattened (Figs. 46, 47). ..... *riparia*
– Tibial apophysis round or oval in cross section (Figs. 24, 26, 30, 40, 56, 62). 9
9(8) Patellar spur broad and jagged (Figs. 62, 63). ..... *procteri*
– Patellar spur pointed (Figs. 24, 26, 30, 40, 56). 10
10(9) Length of patellar spur about equal to the width of its base (Figs. 24, 40, 56). 12
– Length of patellar spur at least two times the width of its base (Figs. 26, 30). 11
11(10) Length of patellar spur two times as great as the width of its base (Figs. 26, 27); three retromarginal teeth on each chelicera; all legs similar. ..... *coconino*
– Length of patellar spur four times as great as the width of its base (Figs. 30 31); two retromarginal teeth on each chelicera;

first two pair of legs with double row of tubercles on venter of robust femur and tibia. ..... *gosiuta*

12(10) Tibial apophysis abruptly bent so that it is nearly parallel to the long axis of the tibia (Figs. 40, 41). ..... *mulaiki*

– Tibial apophysis gradually curved to form a 45° angle with the long axis of the tibia (Figs. 24, 56). 13

13(12) Patellar spur conical (Figs. 24, 25); one retromarginal tooth on each chelicera; first two pair of legs with double row of tubercles on venter of robust femur and tarsus; southeastern Arizona and southern Colorado. ..... *crandalli*

– Patellar spur curved (Figs. 56, 57); two retromarginal teeth on each chelicera; all legs similar; California. ..... *santana*

Key to the Female *Neoantistea*

(Females of *N. coconino* and *N. procteri* are not known)

1 Epigyneal openings in anterior one-half of epigynum; bursae separate (Figs. 22, 23, 34, 35). 2

– Single epigyneal opening in posterior one-fourth of epigynum; bursae fused to form a common canal (Figs. 76, 77). ..... *unifistula*

2(1) Epigyneal openings anterior to or at the same level as the anterior-most loops of the ducts visible in uncleared epigynum (Figs. 20, 54, 64, 66, 70). 3

– Epigyneal openings posterior to the anterior-most loops of the ducts visible in uncleared epigynum (Figs. 32, 38, 48). 11

3(2) Epigyneal openings in a common depression from which protrudes a pointed, flattened scape (Figs. 70, 71). ..... *spica*

– Epigyneal openings separate (Figs. 54, 72), or if adjacent without scape (Figs. 64, 66). 4

4(3) Without bulbs, spermathecae large and bulbous, about three-fourths as long as the epigynum; ducts short and uncoiled (Figs. 66, 67). ..... *inaffecta*

– With bulbs, spermathecae length never more than one-half that of epigyneal length; ducts form at least a simple loop (Figs. 23, 45, 73). 5

5(4) Bulbs about equal in size with spermathecae (Figs. 44, 45, 64, 65). 6

– Bulbs much smaller than spermathecae (Figs. 23, 73). 7

6(5) Spermathecae oval; epigyneal openings at same level as bulbs (Figs. 64, 65); southern Mexico. ..... *hidalgoensis*

– Spermathecae appear as slightly enlarged ducts; epigyneal openings anterior to bulbs (Figs. 44, 45); Oklahoma. ..... *oklahomensis*

7(5) Ducts one-half as wide as a spermatheca (Figs. 72, 73). ..... *magna*

– Ducts one-fifth as wide as a spermatheca or less (Figs. 15, 23, 29, 55). 8

8(7) Spermathecae comma-shaped; ducts form two median loops between spermathecae (Figs. 23, 29). 9

– Spermathecae round or oval; ducts irregularly looped and coiled (Figs. 15, 21, 55). 10

9(8) Ducts about one-fifth as wide as spermatheca; bulbs located anterior and lateral to spermathecae; anterior portion of ducts simple (Figs. 22, 23). ..... *crandalli*

– Ducts about one-eighth as wide as spermatheca; bulbs located anterior to spermathecae; anterior portion of each duct makes two abrupt loops before connecting to the spermatheca (Figs. 28 29). ..... *gosiuta*

10(8) Bulbs about two-fifths as wide as spermathecae, located anterior and lateral to spermathecae (Figs. 54, 55). ..... *santana*

– Bulbs about one-fifth as wide as spermathecae, located anterior to spermathecae (Figs. 14–17, 20, 21). ..... *agilis*

11(2) Bulbs smaller than spermathecae (Figs. 39, 49, 61). 12

– Bulbs nearly equal in size to, or larger than spermathecae (Figs. 33, 35, 53). 14

12(11) Each epigyneal opening in a medially-directed "C" formed by one of the ducts (Figs. 38, 60); bulbs three-fifths as wide as the spermathecae (Figs. 39, 61). 13

– Epigyneal openings in an anteriorly-directed "U" formed by both ducts (Fig. 48); bulbs one-third as wide as the spermathecae (Fig. 49). ..... *riparia*

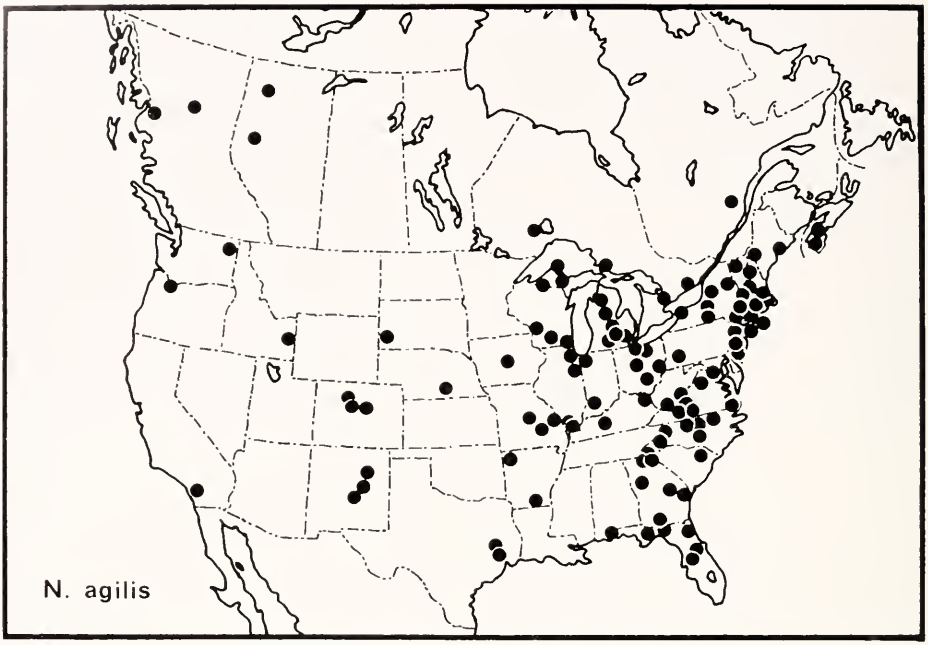
13(12) Ducts long, highly convoluted and asymmetrical (Figs. 38, 39); three retromarginal teeth on each chelicera; Arizona, Texas, Mexico. ..... *mulaiki*

– Ducts short, simple, looped, and symmetrical (Figs. 60, 61); one retromarginal tooth on each chelicera; northern Florida. ..... *alachua*

14(11) Bulbs about three times as large as spermathecae; ducts form a lyre-shaped pattern (Figs. 52, 53). ..... *lyrica*

– Bulbs about the same size as spermathecae 15

15(14) Bulbs cylindrical, separated by a distance equal to the width of each; epigyneal openings separated by a distance two times as great as the length of each (Figs. 32, 33). ..... *jacalana*



Map 2. Distribution of *Neoantistea agilis* (Keyserling).

– Bulbs oval, contiguous or nearly so; epigyneal openings separated by a distance one-half as great as the length of each (Figs. 34, 35). ..... *pueblensis*

Neoantistea agilis (Keyserling) Figures 1–3, 14–21; Map 2

Hahnia agilis Keyserling, 1887, Verh. Zool. Bot. Ges. Wien, 37: 465–467, pl. 4, figs. 29–29a, 29b, ♂, ♀. Male and female syntypes (U.S.N.M. No. 1602, epigynum of female missing) from Fort Stevenson, South Dakota, female syntype (U.S.N.M. No. 1603) from Washington, D.C., all collected by Marx. In United States National Museum collection, housed in American Museum of Natural History, examined.

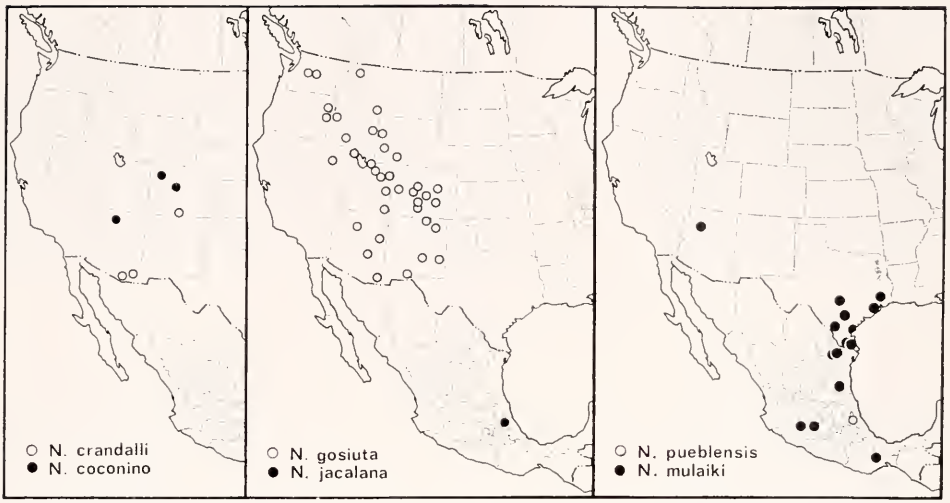
Hahnia bimaculata Emerton, 1890, Trans. Conn. Acad. Arts, Sci., 8: 196, pl. 7, figs. 8, 8c–f; 8a–b, ♀, ♂. Male and two immature syntypes from Salem, Massachusetts. Female syntype from base of Mt. Washington, New Hampshire, in Museum of Comparative Zoology, examined.

Neoantistea agilis, – Gertsch, 1934, Amer. Mus. Novitates, No. 712: 19–23, figs. 29, 41.

Neoantistea gertschi Muma, 1945, Proc. Biol. Soc. Washington, 58: 101–102, figs. 18, 19, ♀. Female holotype from Berwyn, Maryland, in American Museum of Natural History, examined. NEW SYNONYMY.

Description. Total length 2.50 to 3.21 mm, females generally larger than males. Legs banded, dorsum of abdomen with five light chevrons (Fig. 2). Carapace 1.35 mm long, 1.16 mm wide. Eye ratio AME: ALE:PME:PLE = 1:1:0.8:0.8 (Fig. 3). Length and width of sternum about 0.80 mm. Labium 0.18 mm long, 0.25 mm wide. Most specimens have three retromarginal teeth on each chelicera; although one male had four and one female two. Abdomen 1.67 to 2.11 mm long. Distance from spiracle to spinnerets 2.1 times the distance from spiracle to epigastric furrow in male, 2.3 times in female. Proximal segment of lateral spinneret 1.1 times as long as distal segment in male, 1.0 times in female.

Diagnosis. Males may be distinguished from all other species except *N. alachua* and *N. oklahomensis* by a tibial apophysis with the basal two-thirds nearly perpendicular to the long axis of the tibia and



Map 3. Distribution of *Neoantistea crandalli* Gertsch, *Neoantistea coconino* Chamberlin and Ivie, *Neoantistea gosiuta* Gertsch, *Neoantistea jacalana* Gertsch, *Neoantistea pueblensis* n. sp., and *Neoantistea mulaiki* Gertsch.

by a narrow, curved patellar spur about one-half as long as the tibial apophysis (Figs. 18, 19). The patellar spur of *N. agilis* gradually curves to form a 45° angle with the long axis of the patella while the patellar spur of *N. alachua* (Figs. 58, 59) and *N. oklahomensis* (Figs. 42, 43) are more abruptly bent and nearly parallel with the long axis of the patella. Most *N. agilis* males have three retromarginal teeth on each chelicera while *N. alachua* has only one. Females of *N. agilis* (Figs. 14, 15) are similar to those of *N. crandalli* (Figs. 22, 23) and *N. gosiuta* (Figs. 28, 29), but differ from both by having oval rather than comma-shaped spermathecae and ducts which are much more highly convoluted and less symmetrical.

Variation. Of *N. gertschi,* Muma (1945) states, "This species is almost identical in structure and coloration with *N. agilis* (Keyserling). It may be separated from the latter by differences in the details of the epigynum." While uncleared epigyna of "*N. gertschi*" are distinguishable from those of most *N. agilis*, cleared epigyna of the two show little difference (Figs. 14, 15, 20, 21). Others (Emerton, 1890; Gertsch, 1934; and Kaston, 1948) have recognized considerable variability in the arrangement of the highly convoluted portion of the ducts of *N. agilis,* and *N. gertschi* seems to fall within this range of variability. *Neoantistea gertschi* variety females have been collected only east of the Appalachian mountains and are more common in the southern states, indicating speciation. *Neoantistea gertschi* variety females were often found with large collections of *N. agilis* from Pennsylvania, along with females whose epigynal features were intermediate between these two (Fig. 17). The same collections contained only males of the *N. agilis* variety. Of the total 240 females of *N. agilis* and *N. gertschi* variety examined, 45 (19%) were *N. gertschi* variety. *N. gertschi* variety females comprised two of 20 (10%) from New York, one of six (17%) from Connecticut, 20 of 57 (35%) from Pennsylvania, four of 13 (31%) from New Jersey, and five of six (83%) from Georgia and Florida.

Distribution. Throughout the United States and Canada (Map 2).

Neoantistea crandalli Gertsch
Figures 22–25; Map 3

Neoantistea crandalli Gertsch, 1946, J. New York Ent. Soc., 54(3): 35–36, pl. 1, figs. 7, 8, ♂, ♀. Male holotype and paratype from Patagonia, Arizona, in American Museum of Natural History, two male paratypes examined.

Description. Total length 4.00 to 5.10 mm. Legs banded, dorsum of abdomen with five faint chevrons. Carapace 1.70 to 3.40 mm long, 1.60 to 2.30 mm wide. Eye ratio AME:ALE:PME:PLE = 1:1:0.8:0.8. Length and width of sternum about 1.20 mm. Labium 0.26 mm long, 0.40 mm wide. Each chelicera of male with one large retromarginal tooth, female with three. Abdomen 2.36 to 3.13 mm long. Distance from spiracle to spinnerets 2.3 times the distance from spiracle to epigastric furrow in male, 3.3 times in female. Proximal segment of lateral spinnerets 0.9 times as long as distal segment in male, 1.0 times in female.

Diagnosis. Neoantistea crandalli males (Figs. 24, 25) resemble those of *N. santana* (Figs. 56, 57) in their gradually curved tibial apophysis which forms a 45° angle with the long axis of the tibia and patellar spur which has a length about equal to the width of its base. *Neoantistea crandalli* has a conical rather than hooked patellar spur and two rows of tubercles on the venter of the femur and tarsus of the first two pair of legs. All legs of *N. santana* are similar. Females of *N. crandalli* (Figs. 22, 23) resemble those of *N. agilis* (Figs. 14, 15) and *N. gosiuta* (Figs. 28, 29). They differ from *N. agilis* by having comma-shaped rather than oval-shaped spermathecae and less convoluted ducts. They differ from *N. gosiuta* by having bulbs located anterior and lateral to the spermathecae rather than anterior to the spermathecae, by having ducts which are one-fifth rather than one-eighth as wide as each spermathecae, and by lacking a double loop in the anterior portion of each duct.

Distribution. South central Colorado and southeastern Arizona (Map 3).

Neoantistea coconino Chamberlin and Ivie
Figures 26, 27; Map 3

Neoantistea coconino Chamberlin and Ivie, 1942, Bull. Univ. Utah, 32(13): 28–29, pl. 6, figs. 59, 60. Male holotype from Kaibab Forest, Coconino Co., Arizona, in American Museum of Natural History, examined.

Description. Total length of male (female not known) 3.80 mm. Legs banded, dorsum of abdomen with six light, narrow chevrons. Carapace 1.66 mm long, 1.60 mm wide. Eye ratio AME:ALE:PME:PLE = 1:1.1:0.9:1. Sternum 1.00 mm long, 1.11 mm wide. Labium 0.27 mm long, 0.32 mm wide. Each chelicera with three subequal retromarginal teeth. Distance from spiracle to spinnerets 2.2 times the distance from spiracle to epigastic furrow. Proximal segment of lateral spinnerets 1.2 times as long as distal segment.

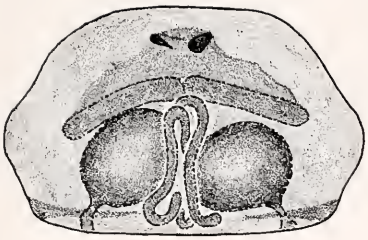
Diagnosis. Males of *N. coconino* (Figs. 26, 27) are similiar to those of *N. gosiuta* (Figs. 30, 31), both having a tibial apophysis which is gradually curved to form a 45° angle with the long axis of the tibia and a narrow, hooked patellar spur. The first two pair of legs of *N. gosiuta* are robust and bear two rows of tubercles on

→

Figures 14–21. *Neoantistea agilis* (Keyserling). 14. Ventral view of epigynum. 15. Dorsal view of cleared epigynum. 16–17. Ventral view of epigynum. 18. Dorsal view of left male palpus. 19. Ventral view of left male palpus. 20. Ventral view of epigynum (holotype of *Neoantistea gertschi* Muma). 21. Dorsal view of cleared epigynum shown in Figure 20.

Figures 22–25. *Neoantistea crandalli* Gertsch. 22. Ventral view of epigynum. 23. Dorsal view of cleared epigynum. 24. Dorsal view of right palpus of male paratype. 25. Ventral view of right palpus of male paratype.

Figures 26–27. *Neoantistea coconino* Chamberlin and Ivie. 26. Dorsal view of left palpus of male holotype. 27. Ventral view of left palpus of male holotype.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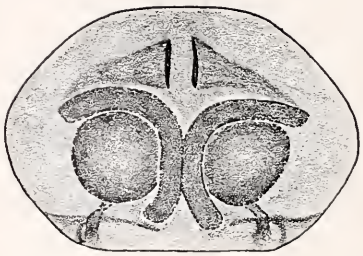
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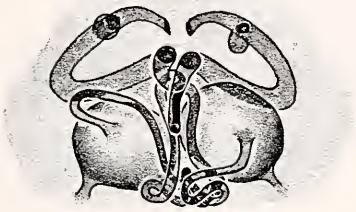
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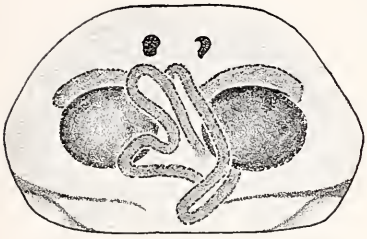
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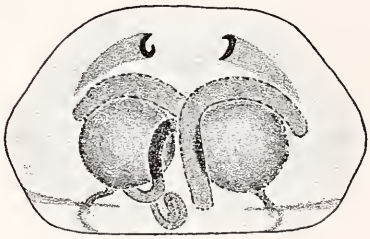
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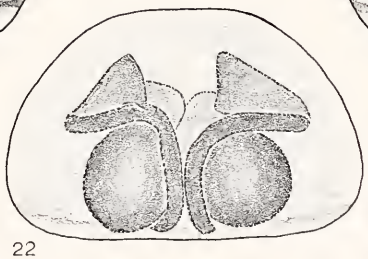
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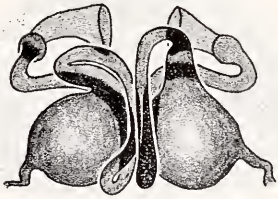
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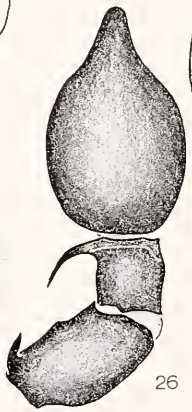
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venter of the femur and tarsus, while in *N. coconino* the first two pair of legs are similar to the other legs.

Distribution. Northern Arizona and northwestern Colorado (Map 3).

Neoantistea gosiuta Gertsch
Figures 28–31; Map 3

Halnia radula, – Chamberlin and Ivie, 1933, Bull. Univ. Utah, 23(2): 48. Not *Halnia radula* Emerton.

Neoantistea gosiuta Gertsch, 1934, Amer. Mus. Novitates, No. 712: 19, 24, figs. 30, 42, ♂, ♀. Male holotype from east of Yost, Utah (University of Utah collection), female paratypes from South Fork of Raft River, eight miles S. of Lynn, Utah, all in American Museum of Natural History, two female paratypes, examined.

Description. Total length 2.62 to 4.10 mm, females generally larger than males. Legs with very faint bands, dorsum of abdomen with six light chevrons. Carapace 1.24 mm long, 1.10 mm wide. Eye ratio AME:ALE:PME:PLE = male 1:0.9:0.8:0.8, female, 1:1:0.8:0.8. Length and width of sternum about 0.80 mm. Labium 0.18 mm long, 0.25 mm wide. Males with two subequal retromarginal teeth on each chelicera, females with two or three. Abdomen 1.64 to 2.77 mm long. Distance from spiracle to spinnerets 2.3 times the distance from spiracle to epigastric furrow in male, 2.1 times in female. Proximal segment of lateral spinnerets 1.0 times as long as distal segment in male, 0.9 times in female.

Diagnosis. Males of *N. gosiuta* (Figs. 30, 31) are similar to those of *N. coconino* (Figs. 26, 27), as both have a tibial apophysis which is gradually curved to form a 45° angle with the long axis of the tibia and a patellar spur which is narrow and hooked. *Neoantistea gosiuta* males are distinguished from those of *N. coconino* by the presence of two rows of tubercles on the venter of robust femur and tarsus of the first two pair of legs. Female *N. gosiuta* (Figs. 28, 29) are similar to those of *N. agilis* (Figs. 14, 15) and *N. crandalli* (Figs. 22, 23). *Neoantistea gosiuta* females differ from *N. agilis* females by having comma-shaped rather than oval spermathecae and by having less convoluted ducts and from *N. crandalli* females by having bulbs located anterior to rather than anterior and lateral to the spermathecae, by having ducts which are one-eighth as wide as a spermathecae rather than one-fifth as wide, and by having two loops in the anterior region of each duct.

Distribution. New Mexico and Arizona northwest to Washington and northwestern Montana (Map 3).

Neoantistea jacalana Gertsch
Figures 32, 33; Map 3

Neoantistea jacalana Gertsch, 1946, J. New York Ent. Soc., 54(3): 32–33, pl. 1, fig. 2. Female holotype and female paratype from Hidalgo, Mexico, 20 mi. S. of Jacalana, in American Museum of Natural History, examined.

Description. Total length of female (males not known) 3.13 to 3.60 mm. Legs banded, dorsum of abdomen with five or six faint chevrons. Carapace 1.35 mm long, 1.13 mm wide. Eye ratio AME:ALE:PME:PLE = 1:1.1:1:1. Length and width of sternum about 0.80 mm. Labium 0.18 mm long, 0.26 mm wide. Each chelicera with three subequal retromarginal teeth. Abdomen 2.18 mm long. Distance from spiracle to spinnerets 2.0 times the distance from spiracle to epigastric furrow. Proximal segment of lateral spinnerets 1.3 times as long as distal segment.

Diagnosis. Females of *N. jacalana* (Figs. 32, 33) are similar to those of *N. pueblensis* (Figs. 34, 35) and *N. riparia* (Figs. 48, 49), but are distinguished from *N. riparia* by the presence of bulbs which are nearly as large as the spermathecae and from *N. pueblensis* by the presence of elongate, separate bulbs rather than oval, contiguous bulbs and by epigyneal openings which are separated by twice rather than one-half the length of each.

Distribution. Eastern central Mexico (Map 3).

Neoantistea pueblensis n. sp.
Figures 34–37; Map 3

Types. Female holotype, male and five female paratypes from 4.4 miles S.W. of Huachinango, Mexico at an elevation of 1700 m, collected in malt traps placed in a moist ravine of an oak forest from 25–28 July 1969 by S. and J. Peck. In the American Museum of Natural History. This species is named for the Mexican state in which the types were collected.

Description. Total length 2.30 to 3.05 mm, females larger than male. Legs not banded, dorsum of abdomen with five light chevrons, lateral surfaces of abdomen of one male and one female with four dark diagonal stripes. Carapace 1.22 mm long, 0.96 mm wide. Eye ratio AME:ALE:PME:PLE = male, 1:1.3:1.3:1.3, female, 1:1.5:1.3:1.5. Sternum 0.64 mm long, 0.72 mm wide. Labium 0.15 mm long, 0.23 mm wide. Each chelicera with four retromarginal teeth (one large and three small). Abdomen 1.28 to 1.93 mm long. Distance from spiracle to spinnerets 1.7 times the distance from spiracle to epigastric furrow in male, 1.9 times in female. Proximal segment of lateral spinnerets 1.2 times as long as distal segment in male, 1.1 times in female.

Diagnosis. Males of *N. pueblensis* (Figs. 36, 37) are distinguished by having a tibial apophysis which is nearly perpendicular to the long axis of the tibia for the basal two-thirds of its length and is two times as long as the tibia is wide. Females of *N. pueblensis* (Figs. 34, 35) are similar to those of *N. jacalana* (Figs. 32, 33) and *N. riparia* (Figs. 48, 49), but are distinguished from the former by having oval, contiguous bulbs rather than elongate, separate bulbs and epigyneal openings separated by a distance equal to one-half rather than twice the length of an opening and from the latter by having bulbs which are equal in size with the spermathecae rather than being only one-fifth their size.

Distribution. Eastern central Mexico (Map 3).

Neoantistea mulaiki Gertsch
Figures 38–41; Map 3

Neoantistea mulaiki Gertsch, 1946, J. New York Ent. Soc., 54(3): 34–35, pl. 1, figs. 5, 6, ♂, ♀. Male holotype and female paratypes from Monterrey, Mexico, in American Museum of Natural History, examined.

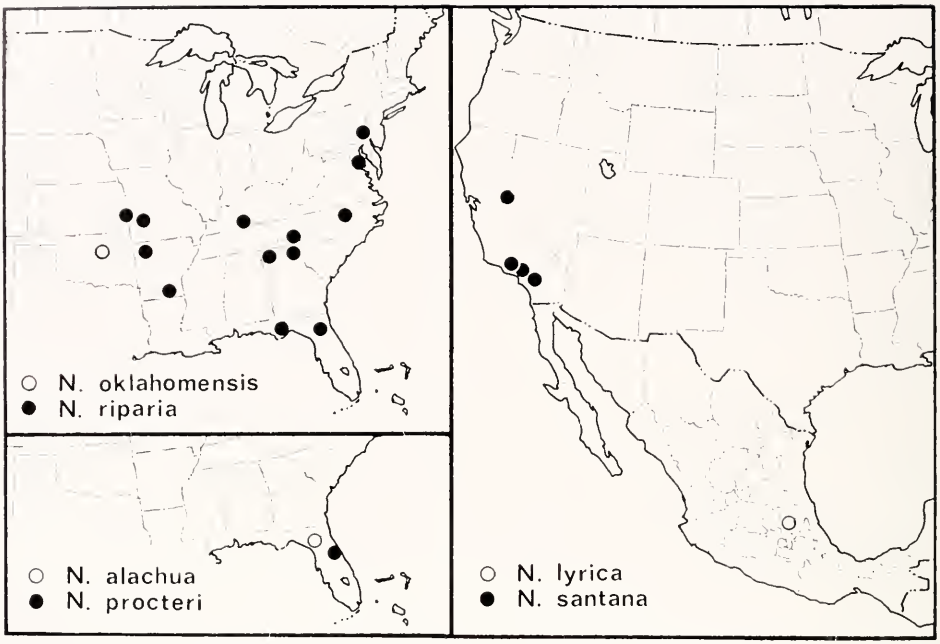
Description. Total length 4.00 to 4.76 mm, male larger than female. Legs banded, dorsum of abdomen with six light chevrons. Carapace of males 2.27 mm long, 1.93 mm wide, of female 1.43 mm long, 1.41 mm wide. Eye ratio AME:ALE:PME:PLE = 1:0.9:0.8:0.9. Length and width of sternum of male 1.30 mm, of female 0.94 mm. Labium of male 0.30 mm long, 0.42 mm wide, of female 0.20 mm long, 0.30 mm wide. Each chelicera of male with one retromarginal tooth, of female with three retromarginal teeth. Abdomen 2.71 mm long. Distance from spiracle to spinnerets 2.7 times the distance from spiracle to epigastric furrow. Proximal segment of lateral spinnerets 1.2 times as long as distal segment in male, 1.0 times in female.

Diagnosis. Males possess an abruptly bent tibial apophysis nearly parallel to the long axis of the tibia and a hooked patellar spur about equal in length to the width of its base (Figs. 40, 41). Females of *N. mulaiki* (Figs. 38, 39) resemble those of *N. alachua* (Figs. 60, 61), which occurs in Florida, in having each epigyneal opening located in a C-shaped loop of a duct. *N. mulaiki* has ducts which are longer, more convoluted, and less symmetrical than those of *N. alachua*.

Distribution. Southeastern and south central Texas south to southeastern Mexico, west to northwestern Arizona (Map 3).

Neoantistea oklahomensis n. sp.
Figures 42–45; Map 4

Types. Female holotype, two male and one female paratypes from near Ripley, Oklahoma, collected 12 October 1973 by Saint, in Museum of Comparative Zoology. Two male and seven female paratypes from near Ripley, Oklahoma, in Oklahoma State



Map 4. Distribution of *Neoantistea oklahomensis* n. sp., *Neoantistea riparia* (Keyserling) *Neoantistea lyrica* n. sp., *Neoantistea santana* Chamberlin and Ivie, *Neoantistea alachua* Gertsch, and *Neoantistea procteri* Gertsch.

University Entomology Museum. The name of this species is derived from the state where the type specimens were collected.

Description. Total length 2.40 to 3.00 mm. Legs banded, dorsum of abdomen with five light chevrons. Carapace 1.20 mm long, 1.00 mm wide. Eye ratio AME:ALE: PME:PLE = 1:1:0.8:0.8. Length and width of sternum 0.78 mm. Labium 0.17 mm long, 0.24 mm wide. Each chelicera with three retromarginal teeth. Abdomen 1.60 mm long. Distance from spiracle to spinnerets 1.8 times the distance from spiracle to epigastric furrow in male, 2.0 times in female. Proximal segment of lateral spinnerets 1.0 times as long as distal segment.

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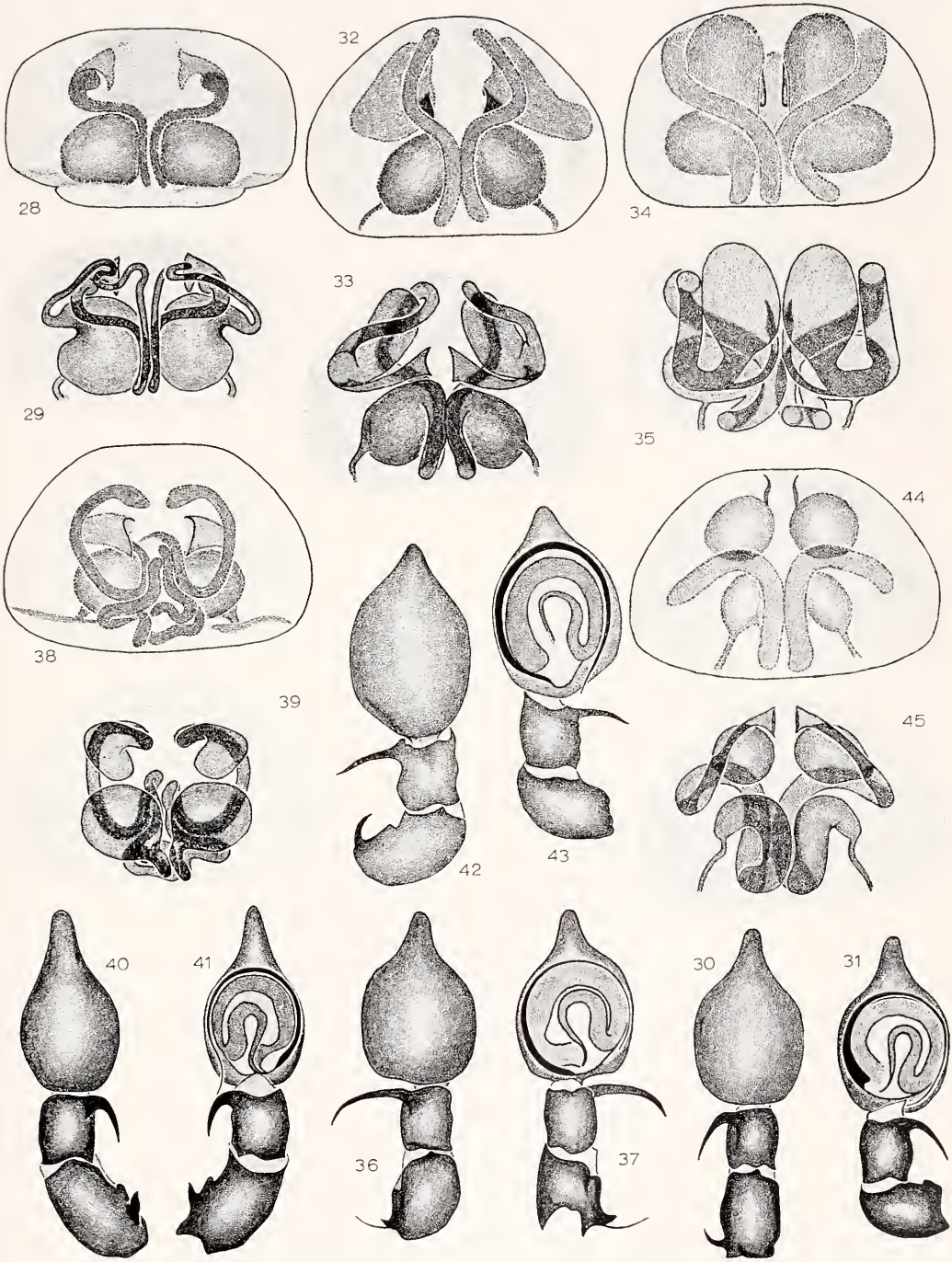
Figures 28–31. *Neoantistea gosiuta* Gertsch. 28. Ventral view of epigynum. 29. Dorsal view of cleared epigynum. 30. Dorsal view of left male palpus. 31. Ventral view of left male palpus.

Figures 32–33. *Neoantistea jacalana* Gertsch. 32. Ventral view of epigynum of holotype. 33. Dorsal view of cleared epigynum of holotype.

Figures 34–37. *Neoantistea pueblensis* n. sp. 34. Ventral view of epigynum of holotype. 35. Dorsal view of cleared epigynum of holotype. 36. Dorsal view of left palpus of male paratype. 37. Ventral view of left palpus of male paratype.

Figures 38–41. *Neoantistea mulaiki* Gertsch. 38. Ventral view of epigynum of paratype. 39. Dorsal view of cleared epigynum of paratype. 40. Dorsal view of right palpus of male holotype. 41. Ventral view of right palpus of male holotype.

Figures 42–45. *Neoantistea oklahomensis* n. sp. 42. Dorsal view of left palpus of male paratype. 43. Ventral view of left palpus of male paratype. 44. Ventral view of epigynum of holotype. 45. Dorsal view of cleared epigynum of holotype.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Diagnosis. A nearly straight tibial apophysis and a long, narrow patellar spur one-half as long as the tibial apophysis and curved nearly parallel to the long axis of the patella distinguishes *N. oklahomensis* males (Figs. 42, 43) from those of all other species except *N. alachua* (Figs. 58, 59). *Neoantistea oklahomensis* has been found only in Oklahoma and has three retromarginal teeth on each chelicera while *N. alachua* has been found only in Florida and has one retromarginal tooth on each chelicera. Females of *N. oklahomensis* (Figs. 44, 45) differ from those of other species by having epigyneal openings located at the anterior margin of the epigynum, spermathecae which appear as slightly enlarged ducts, and bulbs which in an uncleared epigynum appear as large as the spermathecae.

Distribution. Known only from Oklahoma (Map 4).

Neoantistea riparia (Keyserling)
Figures 46–49; Map 4

Hahnia riparia Keyserling, 1887, Verh. Zool. Bot. Ges. Wien, 37: 463–464, pl. 6, fig. 27, ♂. Male syntype from Springdale, Utah, erroneous locality (U.S.N.M. No. 1605), collected by Marx, in United States National Museum Collection, housed in American Museum of Natural History, examined.

Neoantistea barrowsi Gertsch, 1934, Amer. Mus. Novitates, No. 712: 19, 29–31, figs. 36, 37, ♂, ♀. Male holotype from Franklington, North Carolina, in American Museum of Natural History, examined. NEW SYNONYMY.

Note. The Keyserling species *Hahnia riparia* and *Hahnia magna* were incorrectly considered synonyms by earlier workers. This discovery makes proper the synonymy of *Neoantistea riparia* and *Neoantistea barrowsi* and the use of *Neoantistea magna* for specimens previously identified as *N. riparia*, *N. riparia radula*, and *N. radula*.

Description. Total length 3.66 to 4.57 mm. Legs banded, dorsum of abdomen with six light chevrons. Carapace 1.56 to 1.85 mm long, 1.28 to 1.65 mm wide. Eye ratio AME:ALE:PME:PLE = male, 1:0.9:0.6:0.8, female, 1:1:0.8:0.9. Length of sternum 0.92 mm, width 1.02 mm. Labium 0.22 mm long, 0.32 mm wide. Male with one retromarginal tooth on each chelicera, female with three subequal retromarginal teeth. Abdomen 1.80 to 3.39 mm long. Distance from spiracle to spinnerets 2.4 times the distance from spiracle to epigastric furrow in male, 2.6 times in female. Proximal segment of lateral spinnerets 1.0 times as long as distal segment in male, 1.1 times in female.

Diagnosis. Males of *N. riparia* are distinguished from those of all other species by a broad, flattened tibial apophysis and a conical patellar spur with a long seta extending from the tip (Figs. 46, 47). Females of *N. riparia* (Figs. 48, 49) are similar to those of *N. jacalana* (Figs. 32, 33) and *N. pueblensis* (Figs. 34, 35), but can be distinguished from both by bulbs about one-fifth as large, rather than equal to the spermathecae.

Distribution. Eastern Pennsylvania south to northern Florida, west to southeastern Kansas and southeastern Arkansas (Map 4).

Neoantistea lyrica n. sp.
Figures 50–53; Map 4

Types. Female holotype and male and three female paratypes from Cerro Muerte (elevation 10,000 m), Costa Rica, collected 2 August 1966 by S. Peck, in Museum of Comparative Zoology. The name refers to the lyre pattern of the epigynum ducts (Fig. 52).

Description. Total length 3.02 to 3.46 mm. Legs not banded, dorsum of abdomen heavily splotched with dark gray and with four light chevrons in the posterior half. Carapace 1.44 mm long, 1.14 mm wide. Eye ratio AME:ALE:PME:PLE = male, 1:1.2:1:1.2, female, 1:1.3:1.3:1.5. Length and width of sternum 0.80 mm. Labium 0.19 mm long, 0.25 mm wide. Each chelicera with three subequal retromarginal teeth. Abdomen 1.68 to 2.10 mm long. Distance from spiracle to spinnerets 1.8 times the distance from spiracle to epigastric furrow.

Proximal segment of lateral spinnerets 1.1 times as long as distal segment.

Diagnosis. Males of *N. lyrica* are distinguished from those of all other species by the absence of a patellar spur (Figs. 50, 51). The distinctive lyrelike arrangement of the ducts of the epigynum (Fig. 52) and the presence of bulbs which are three times as large as the spermathecae (Fig. 53) separate females of *N. lyrica* from those of all other species.

Distribution. Southern central Mexico (Map 4).

Neoantistea santana Chamberlin and Ivie
Figures 54–57; Map 4

Neoantistea santana Chamberlin and Ivie, 1942, Bull. Univ. Utah, 32(13): 29, pl. 6, figs. 61–62, 63, ♂, ♀. Male holotype from Laguna Beach, Orange Co., California, in American Museum of Natural History, male and female paratypes examined.

Neoantistea jollensis Schenkel, 1950, Verhandl. Naturf. Gesell., Basel, 61: 90, fig. 34, ♀. Female holotype from Country Club Heights, LaJolla, San Diego Co., California, in Naturhistorisches Museum, Basel, Switzerland, examined. NEW SYNONYMY.

Description. Total length 4.36 to 4.62 mm. Legs banded, dorsum of abdomen with five or six light chevrons. Carapace 1.52 mm long, 1.42 mm wide. Eye ratio AME:ALE:PME:PLE = 1:1:0.9:0.9. Sternum 0.96 mm long, 1.15 mm wide. Labium 0.27 mm long, 0.36 mm wide. Each chelicera of male with two retromarginal teeth, of female with three retromarginal teeth. Abdomen of male 2.54 mm long, of female 3.18 mm long. Distance from spiracle to spinnerets 1.8 times the distance from spiracle to epigastric furrow in male, 1.3 times in female. Proximal segment of lateral spinnerets 1.4 times as long as distal segment in male, 1.3 times in female.

Diagnosis. Males of *N. santana* have a tibial apophysis curved to form a 45° angle with the long axis of the tibia and a patellar spur which is about as long as its base is broad (Figs. 56, 57), making them similar to those of *N. crandalli* (Figs. 24, 25). In males of *N. crandalli* the first two pairs of legs are robust and have two rows of tubercles on the ventral surfaces of the femur and tarsus, while in *N. santana* the first two pairs of legs are similar to the others. Females of *N. santana* (Figs. 54, 55) are distinguished by their asymmetrical, highly coiled ducts and laterally located bulbs which are two-fifths as wide as the spermathecae.

Distribution. Central and southern California (Map 4).

Neoantistea alachua Gertsch
Figures 58–61; Map 4

Neoantistea alachua Gertsch, 1946, J. New York Ent. Soc., 54: 33–34, figs. 3, 4, ♂, ♀. Male holotype from 5 mi. W. of Gainesville, Alachua Co., Florida, in American Museum of Natural History, examined.

Description. Total length of male 2.78 mm, of female 3.46 mm. Legs banded, dorsum of abdomen with four light chevrons. Carapace 1.09 mm long in male, 1.43 mm long in female. Width of carapace 1.09 mm in male, 1.17 mm in female. Eye ratio AME:ALE:PME:PLE = 1:09:0.7:09. Sternum 0.74 mm long, 0.80 mm wide. Labium 0.17 mm long, 0.23 mm wide. Each chelicera with one retromarginal tooth. Abdomen of male 1.71 mm long, of female 2.31 mm. Distance from spiracle to spinnerets 2.5 times the distance from spiracle to epigastric furrow in male, 2.6 times in female. Proximal segment of lateral spinnerets 1.1 times as long as distal segment.

Diagnosis. The presence of a nearly straight tibial apophysis and a narrow patellar spur which is half as long as the tibial apophysis and is curved to be nearly parallel with the long axis of the patella (Figs. 58, 59) distinguish males of *N. alachua* from all other species except *N. oklahomensis* (Figs. 42, 43). *Neoantistea alachua* has been collected only from Florida and has one retromarginal tooth on each chelicera while *N. oklahomensis* has been collected only from Oklahoma and

has three retromarginal teeth on each chelicera. Females of *N. alachua* (Figs. 60, 61) have the epigyneal openings situated in a "C" formed by each duct, much as in *N. mulaiki* (Figs. 38, 39). *Neoantistea alachua* has short, symmetrical ducts while *N. mulaiki* has much longer, asymmetrically arranged ducts.

Distribution. Known only from Alachua Co. in north central Florida (Map 4).

Neoantistea procteri Gertsch
Figures 62, 63; Map 4

Neoantistea procteri Gertsch, 1946, J. New York Ent. Soc., 54(3): 31–32, pl. 1, fig. 1, ♂. Male holotype from St. John's River near Geneva, Florida, in American Museum of Natural History, examined.

Description. Total length of male (females not known) 3.12 mm. Legs banded, dorsum of abdomen with five light chevrons. Carapace 1.62 mm long, 1.41 mm wide. Eye ratio AME:ALE:PME:PLE = 1:0.7:0.7:0.7. Sternum 0.79 mm long, 0.92 mm wide. Labium 0.20 mm long, 0.29 mm wide. Left chelicera with one retromarginal tooth, right with three subcontiguous retromarginal teeth. Abdomen 1.79 mm long. Distance from spiracle to spinnerets 2.1 times the distance from spiracle to epigastric furrow. Proximal segment of lateral spinnerets 1.4 times as long as distal segment.

Diagnosis. Males of N. *procteri* are distinguished from those of all other species by the presence of a broad, jagged patellar spur (Figs. 62, 63).

Distribution. Known only from the type locality in eastern central Florida (Map 4).

Neoantistea hidalgoensis n. sp.
Figures 64, 65; Map 5

Type. Female holotype from 6.4 mi. S. of Tenango de Doria (elevation 3000 m), Hidalgo, Mexico, collected 24–28 July 1969 from carrion trap in pine-oak forest by S. and J. Peck, in American Museum of Natural History. The name of this species is derived from that of the Mexican state from which the type was collected.

Note. Both the metatarsus and tarsus were missing from legs I–III and leg IV had no tarsus. The leg length is apparently IV, I, II, III.

Description. Total length of female (males not known) 2.71 mm. Legs not banded, dorsum of abdomen with two light chevrons just forward of the anal tubercle, remainder of dorsum with several light blotches on a field of gray. Carapace 1.14 mm long, 0.92 mm wide. Eye ratio AME:ALE:PME:PLE = 1:2:1.7:2. Sternum 0.67 mm long, 0.76 mm wide. Labium 0.17 mm long, 0.24 mm wide. Each chelicera with four retromarginal teeth, one large and three small. Abdomen 1.75 mm long. Distance from spiracle to spinnerets 1.8 times the distance from spiracle to epigastric furrow. Proximal segment of the posterior

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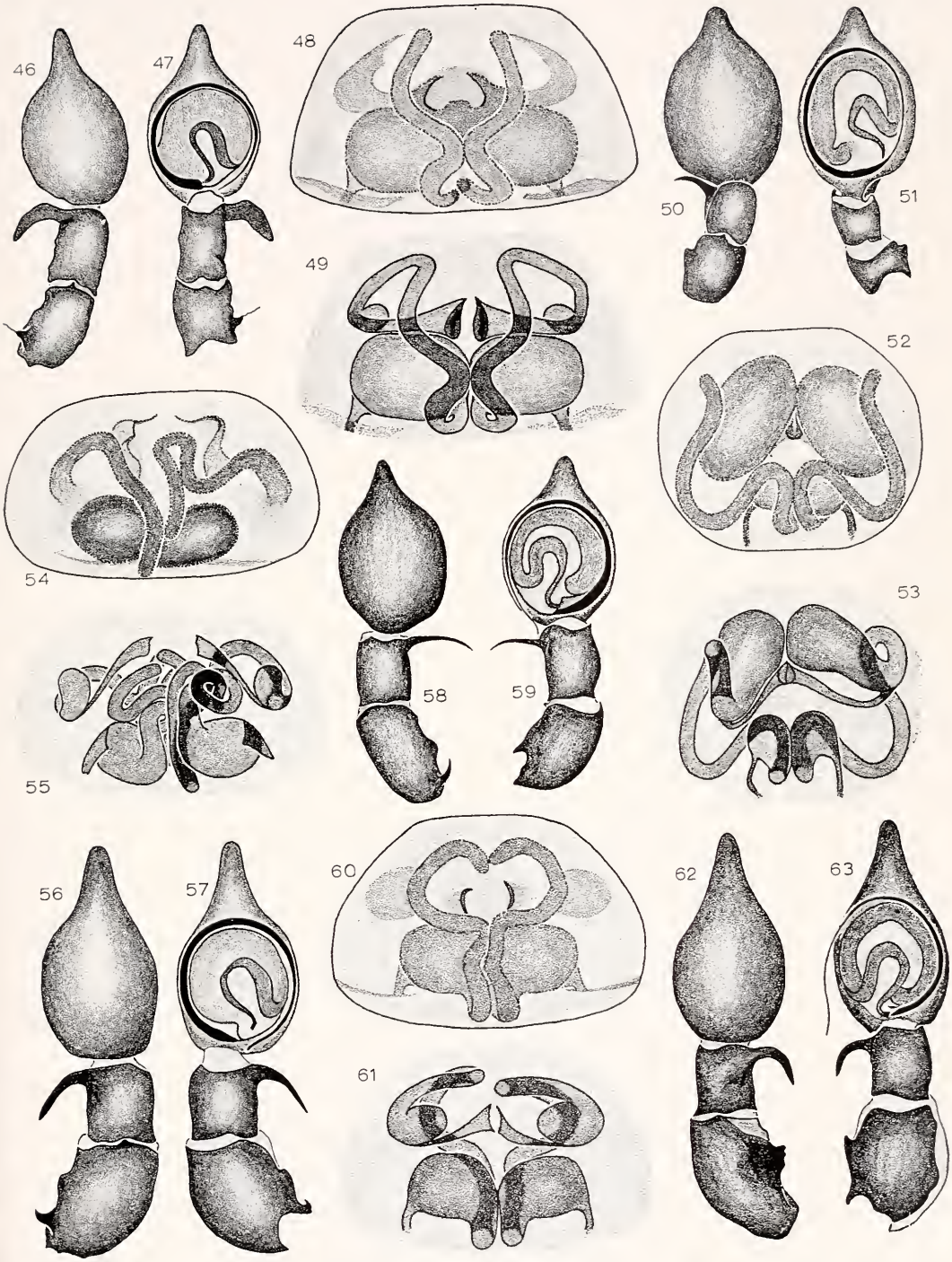
Figures 46–49. *Neoantistea riparia* (Keyserling). 46. Dorsal view of left male palpus. 47. Ventral view of left male palpus. 48. Ventral view of epigynum. 49. Dorsal view of cleared epigynum.

Figures 50–53. *Neoantistea lyrica* n. sp. 50. Dorsal view of left palpus of male paratype. 51. Ventral view of left palpus of male paratype. 52. Ventral view of epigynum of holotype. 53. Dorsal view of cleared epigynum of holotype.

Figures 54–57. *Neoantistea santana* Chamberlin and Ivie. 54. Ventral view of epigynum of paratype. 55. Dorsal view of cleared epigynum of paratype. 56. Dorsal view of left palpus of male holotype. 57. Ventral view of left palpus of male holotype.

Figures 58–61. *Neoantistea alachua* Gertsch. 58. Dorsal view of right palpus of male holotype. 59. Ventral view of right palpus of male holotype. 60. Ventral view of epigynum of paratype. 61. Dorsal view of cleared epigynum of paratype.

Figures 62–63. *Neoantistea procteri* Gertsch. 62. Dorsal view of right palpus of male holotype. 63. Ventral view of right palpus of male holotype.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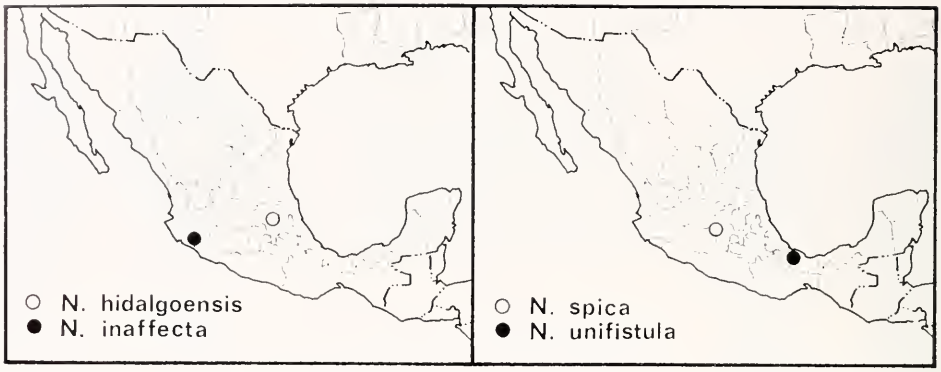


Map 5. Distribution of *Neoantistea hidalgoensis* n. sp., *Neoantistea inaffecta* n. sp., *Neoantistea spica* n. sp., and *Neoantistea unifistula* n. sp.

spinnerets 1.2 times as long as the distal segment.

Diagnosis. Females of *N. hidalgoensis* are distinguished from those of all other species by the arrangement of the ducts to form two posteriorly-directed "C"'s in which the spermathecae lie (Fig. 64), by the equal-sized bulbs and spermathecae (Fig. 65), by the absence of bands on the legs, and by the presence of only two chevrons on the dorsum of the abdomen.

Distribution. Known only from the type locality in south central Mexico (Map 5).

Neoantistea inaffecta n. sp.
Figures 66–69; Map 5

Types. Female holotype and male paratype from Nevado de Colima, Colima, Mexico, collected 20 January 1943 by F. Bonet, in American Museum of Natural History. The name refers to the simple nature of the epigynum.

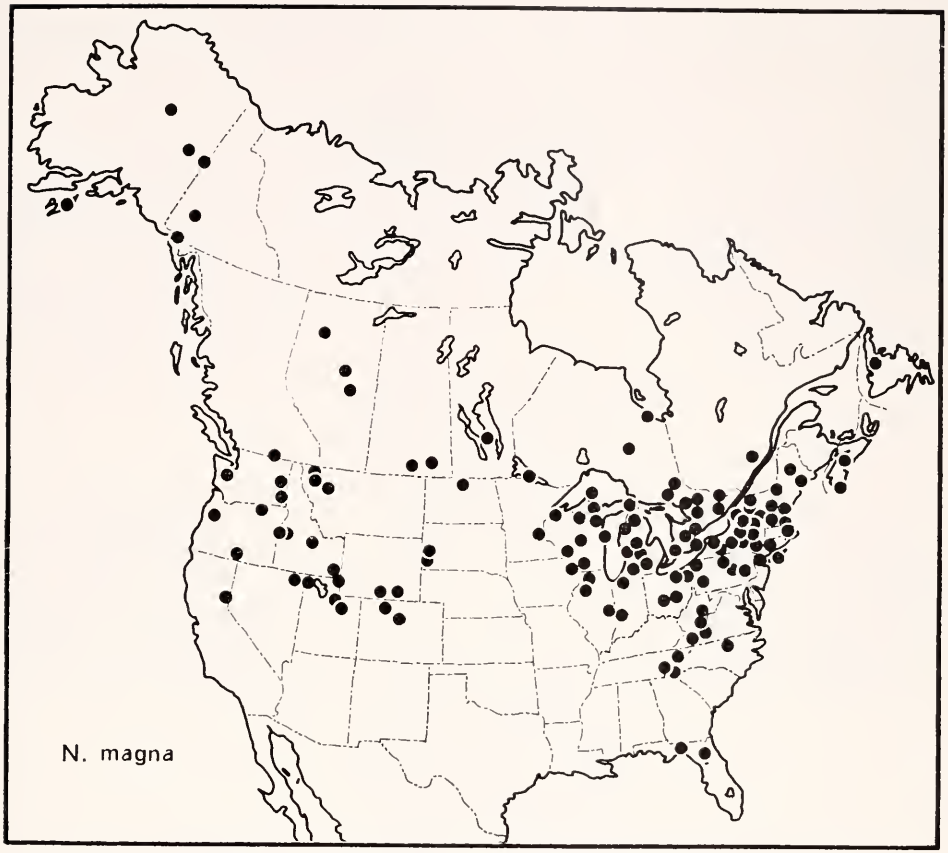
Description. Total length of male 2.2 mm, of female 2.4 mm. Legs banded, dorsum of abdomen with five or six light chevrons. Carapace of male 1.1 mm long, 0.8 mm wide; of female 0.9 mm long, 0.8 mm wide. Eye ratio AME:ALE:PME:PLE = male, 1:1.6:1.2:1.6, female, 1:1.3:1:1.1. Sternum 0.54 mm long, 0.60 mm wide. Labium 0.12 mm long, 0.20 mm wide. Each chelicera of male with four retromarginal teeth, of female with three retromarginal teeth. Abdomen of male 1.3 mm long, of female 1.6 mm long. Distance from spiracle to spinnerets 1.8 times the distance from spiracle to epigastric furrow in male, 1.7 times in female. Proximal segment of lateral spinnerets 1.1 times as long as distal segment.

Diagnosis. Males of *N. inaffecta* (Figs. 68, 69) can be distinguished from those of all other species except *N. magna* (Figs. 74, 75) by the presence of a straight tibial apophysis and a broad patellar spur which is hooked at its tip. Males of *N. inaffecta* have four retromarginal teeth rather than only one, have the embolus held in a groove at the base of the tibial apophysis rather than encircling the cymbium in the usual manner, and are known only from southwestern Mexico rather than from the U. S. and Canada. Females of *N. inaffecta* are distinguished by the absence of bulbs in the epigynum, by short, nearly straight ducts, and by spermathecae which are about three-fourths as long as the epigynum (Figs. 66, 67).

Distribution. Known only from the type locality in southwestern Mexico (Map 5).

Neoantistea spica n. sp.
Figures 70, 71; Map 5

Type. Female holotype from Desiertos de los Leones, Distrito Federal, Mexico, collected 12 June 1946 by J. C. and D. L.



Map 6. Distribution of *Neoantistea magna* (Keyserling).

Pallister, in the American Museum of Natural History. The name refers to the projection of a scape from the depression containing the epigyneal openings.

Description. Total length of female (males are not known) 3.00 mm. Legs banded, dorsum of abdomen with four very thin, light chevrons. Carapace 1.3 mm long, 1.2 mm wide. Eye ratio AME:ALE:PME: PLE = 1:1.2:1.2:1.2. Length and width of sternum 0.82 mm. Labium 0.19 mm long, 0.25 mm wide. Each chelicera with three subequal retromarginal teeth. Abdomen 1.9 mm long. Distance from spiracle to spinnerets 2.1 times the distance from spiracle to epigastric furrow. Proximal segment of lateral spinnerets 1.1 times as long as distal segment.

Diagnosis. The projection of a thin, pointed scape from a shallow depression in which the epigyneal openings are located (Fig. 70) distinguishes females of *N. spica* from those of other species. Separated bulbs which are larger than the oval spermatheeae to which they connect by short ducts (Fig. 71) further distinguish females.

Distribution. Known only from the type locality in southeastern Mexico (Map 5).

Neoantistea magna (Keyserling)
Figures 13, 72–75; Map 6

Hahnia magna Keyserling, 1887, Verh. Zool. Bot. Ges. Wien, 37: 464, pl. 6, fig. 28, ♀. Two female syntypes from Fort Bridger, Wyoming, collected by Marx, in United States National Museum collection housed in the American Museum of Natural History, examined.

Hahnia radula Emerton, 1890, Trans Connecticut Acad. Arts Sci., 8: 196, pl. 7, figs. 10, 10a, ♂. Male holotype from Jaffrey, New Hampshire, in Museum of Comparative Zoology, examined.
Antistea riparia, – Simon, 1898, Histoire Naturelle des Araignées, 2: 274. (misidentification)
Neoantistea riparia, – Gertsch, 1934, Amer. Mus. Novitates, No. 712: 25, figs. 13–17, 38–40, ♂, ♀. (misidentification)
Neoantistea riparia race *radula*, – Gertsch, 1934, Amer. Mus. Novitates, No. 712: 28, fig. 18.
Neoantistea radula, – Kaston, 1948, Bull. St. Geol. Nat. Hist. Surv. Connecticut, 70: 294, figs. 958–959.

Note. Hahnia riparia and *Hahnia magna* have been incorrectly considered synonyms. The name *Neoantistea riparia* has to be used for the species previously known as *Neoantistea barrowsi* and the name *Neoantistea magna* for *N. riparia*, *N. riparia radula*, and *N. radula*.

Discussion. Based upon the equal sizes of the AME and PME Gertsch (1934) recognized the eastern race *N. riparia radula* as distinct from the western *N. riparia* whose AME are larger than the PME. Using this distinction, Kaston (1948) recognized the eastern species *N. radula*. Levi and Field (1954) and Chickering (1963) find this distinction unwarranted and an examination of specimens shows the larger PME to appear sporadically in populations throughout the range of *N. riparia*. No other differences between *riparia* and *radula* were found so the species have been synonymized.

Description. Total length 3.73 mm. Legs banded, dorsum of abdomen with six light chevrons. Carapace 1.54 mm long, 1.35 mm wide. Eye ratio AME:ALE:PME:PLE = male, 1:1:0.8:0.9, female, 1:1:0.8:0.8. Sternum 0.87 mm long, 1.00 mm wide. Labium 0.23 mm long, 0.34 mm wide. Each chelicera of male with one retromarginal tooth, of female with three retromarginal teeth. Abdomen 2.30 mm long. Distance from spiracle to spinnerets 2.2 times the distance from spiracle to epigastric furrow. Proximal segment of lateral spinnerets 1.0 times as long as distal segment.

Diagnosis. Males of *N. magna* have a straight tibial apophysis and a broad patellar spur which is hooked at its tip (Figs. 74, 75), making them similar to those of *N. inaffecta* (Figs. 68, 69). *Neoantistea magna* has one retromarginal tooth on each chelicera while *N. inaffecta* has four retromarginal teeth on each chelicera. *Neoantistea magna* has an embolus which encircles the cymbium in the usual manner while *N. inaffecta* has an embolus which passes through a groove at the base of the tibial apophysis. *Neoantistea magna* is found in the United States and Canada while *N. inaffecta* has been found only in southwestern Mexico. Females of *N. magna* are distinguished by ducts half as wide as each spermatheca and short and simply looped, and by bulbs one-fourth as wide as the spermathecae (Figs. 72, 73).

Distribution. Newfoundland south to northern Florida, west to Alaska and central California (Map 6).

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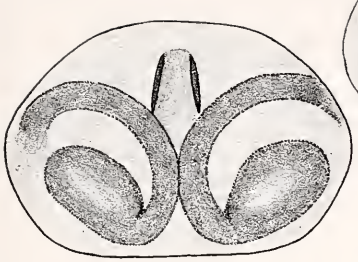
Figures 64–65. *Neoantistea hidalgoensis* n. sp. 64. Ventral view of epigynum of holotype. 65. Dorsal view of cleared epigynum of holotype.

Figures 66–69. *Neoantistea inaffecta* n. sp. 66. Ventral view of epigynum of holotype. 67. Dorsal view of cleared epigynum of holotype. 68. Dorsal view of left palpus of male paratype. 69. Ventral view of left palpus of male paratype.

Figures 70–71. *Neoantistea spica* n. sp. 70. Ventral view of epigynum of holotype. 71. Dorsal view of cleared epigynum of holotype.

Figures 72–75. *Neoantistea magna* (Keyserling). 72. Ventral view of epigynum. 73. Dorsal view of cleared epigynum. 74. Dorsal view of left male palpus. 75. Ventral view of left male palpus.

Figures 76–77. *Neoantistea unifistula* n. sp. 76. Ventral view of epigynum of holotype. 77. Dorsal view of cleared epigynum of holotype.



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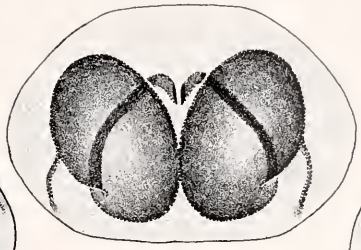

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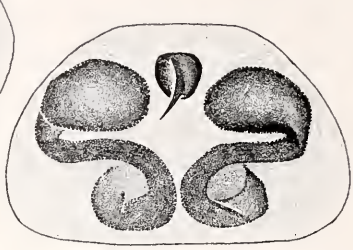

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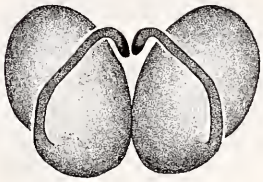

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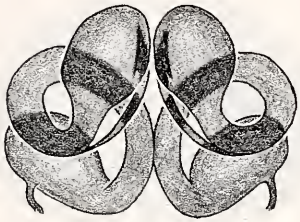

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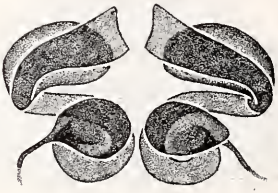

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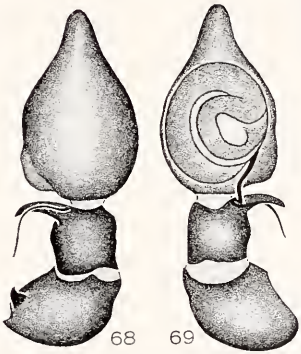

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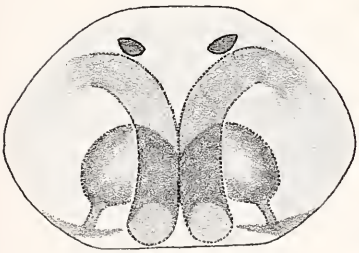

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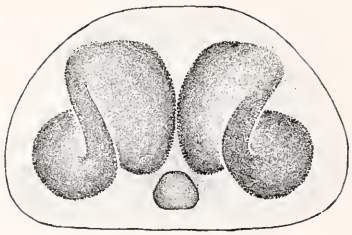

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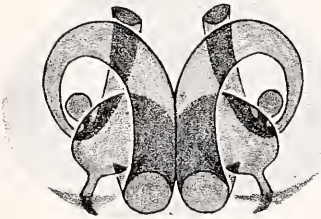

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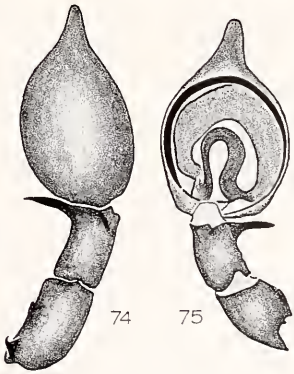

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Neoantistea unifistula n. sp.
Figures 76, 77; Map 5

Type. Female holotype from Sotano de Botella Chica, 2 mi. N.W. of Tequila, Veracruz, Mexico, collected 4 August 1967 by J. Reddell and J. Fish. Female paratype from Volcan San Martín (elevation 3500 feet), Veracruz, collected 14 July 1953 by C. J. Goodnight. Both in American Museum of Natural History. This species is named for the unique fused ducts in the epigynum.

Description. Total length of female (males are not known) 3.00 mm. Legs not banded, dorsum of abdomen with four light chevrons. Carapace 1.30 mm long, 1.00 mm wide. Eye ratio AME:ALE:PME:PLE = 1:2.4:2:2.2. Length and width of sternum 0.73 mm. Labium 0.15 mm long, 0.24 mm wide. Each chelicera with four retromarginal teeth. Abdomen 1.8 mm long. Distance from spiracle to spinnerets 3.0 times the distance from spiracle to epigastric furrow. Proximal segment of lateral spinnerets 1.3 times as long as distal segment.

Diagnosis. Females of *N. unifistula* are distinguished from those of other species by a common epigyneal opening in the posterior one-fourth of the epigynum (Fig. 76) and by ducts (bursae) fused for about half of their length (Fig. 77).

Distribution. Known in the Nearctic only from the holotype from southeastern Mexico (Map 5).

Hahnia C. L. Koch

Hahnia C. L. Koch, 1841, Die Arachniden, 8: 61, figs. 637–638, ♀, ♂. Type species by monotypy: *Hahnia pusilla* C. L. Koch, ibid., from Germany. The generic name is feminine.

Hahnistea Chamberlin and Ivie, 1942, Bull. Univ. Utah, 32(13): 27–28, fig. 58. Type species by original designation and monotypy: *Hahnistea longipes* Chamberlin and Ivie, ibid. NEW SYNONYMY.

Unzickeria Lehtinen, 1967, Ann. Zoologici, 4: 199–496. Type species by original designation: *Hahnia okefinokensis* Chamberlin and Ivie, 1934, in Gertsch, Amer. Mus. Novitates, No. 712: 1–32, figs. 22, 23, ♂. NEW SYNONYMY.

Diagnosis. Hahnia is characterized by having the spiracular opening twice as far from the epigastric furrow as from the base of the median spinnerets (Figs. 10, 11) (in *H. flaviceps* the spiracle may be about midway between the epigastric furrow and bases of the median spinnerets), by having the distal segment of each lateral spinneret about two-thirds as long as the proximal segment (Figs. 10, 11), and by having the AME smaller than the PME (Fig. 12).

The nine species of Nearctic *Hahnia* appear to constitute three species groups. *Hahnia arizonica, H. cinerea,* and *H. ononidum* form a compact group whose male members have a palp with a recurved tibial apophysis, a brush of setae on the ventral margin of the cymbium, and a transparent cymbial conductor and whose female members have an epigynum with equal-sized bulbs and spermathecae, ducts of an intermediate length, and epigyneal openings in the posterior one-third of the epigynum. *Hahnia sanjuanensis, H. glacialis, H. flaviceps,* and *H. veracruzana* form a somewhat less compact group whose male members have a palp with a long, slightly curved tibial apophysis, no brush of setae or conductor and whose female members have an epigynum without bulbs, with long ducts, and with epigyneal openings in the anterior one-third of the epigynum. *Hahnia nobilis* and *H. okefinokensis* are closely similar species whose members are smaller than those of other species in this genus, whose male members have a short, slightly curved tibial apophysis and a palp without a brush of setae or conductor and whose female members have an indistinct epigynum without bulbs, with short or intermediate length ducts, and with epigyneal openings in the center of the epigynum. Although the genus *Hahnia* appears more diverse than either *Antistea* or *Neoantistea*, there seems at present no basis for placing any of the above species or species groups into another genus as Chamberlin and Ivie (1942) and Lehtinen (1967) propose.

Chamberlin and Ivie (1942) separated

Hahnistea from other hahniid genera by their possession of longer legs, an eye ratio of AME:ALE:PME:PLE = 1:2:1.6:2, a slightly procurved anterior eye row and a straight posterior eye row, a spiracle which is "about midway" between the spiracle and genital furrow, and lateral spinnerets whose distal segments are about one-half as long as their proximal segments.

Hahnia sanjuanensis appears to fall within the limits of the genus *Hahnia* as it is defined here. Although its legs are longer than most *Hahnia* they are similar to those of *H. glacialis*. The spiracle of specimens examined was more posterior than Chamberlin and Ivie indicate and falls within the range described for *Hahnia*, as do the eye configuration and spinneret segment lengths.

Lehtinen (1967) placed *Hahnia okefinokensis, Bigois tatei* Gertsch, and *Hahnia ernesti*, – Petrunkevitch into a new genus, *Unzickeria*, which he characterized primarily by features of the genitalia. These species do not appear to form a very uniform genus. As Gertsch (1934) describes, *B. tatei* differs from both *H. ernesti* and *H. okefinokensis* by having AME one-fifth the diameter of the ALE, rather than half the diameter and by having the proximal segment of the intermediate (second) spinnerets longer than the corresponding segment of the lateral spinnerets.

Hahnia veracruzana and *H. ernesti* Simon are placed in the genus *Neohahnia* Mello-Leitão, 1917, by Lehtinen (1967). Although females of *H. veracruzana* are not known, the male genitalia of this species are closer to those of some species Lehtinen retains in the genus *Hahnia* than to *H. ernesti* Simon, and there seems no reason to remove *H. veracruzana* from the genus *Hahnia*.

Coloration. Carapace of most species brown with darker bands radiating from the cervical groove. A dark patch on the posterior cephalic region helps form a U-shaped marking which delineates the cephalic region. Chelicerae are reddish brown. Endites and labium are brown. Sternum is tan, often with a gray margin. Leg segments brown, becoming lighter towards either end in some specimens. Palp segments are brown. Dorsum of abdomen tan, splotched with gray to form five to seven light, median chevrons in most species. The anterior two or three chevrons are commonly divided by a median gray line. Two small, light dots often lie forward of the anterior chevron. Oblique rows of small dots are found on the lateral surfaces of the abdomen. Venter of the abdomen in most species is tan. Spinneret segments are tan.

Structure. Total length ranges from 1.17 to 2.38 mm, of which the abdomen comprises about two-thirds. Cephalic region of carapace about two-thirds as wide as thoracic region. Maximum width of carapace equal to carapace length. Anterior and posterior eye rows about equally procurved. Median ocular quadrangle narrower anteriorly. AME 0.25 to 0.75 times as large as PME; PME 1.33 to 4.00 times further apart than are AME. Each chelicera about one-half as wide as long with one to five retromarginal teeth. Endites nearly equal in width and length. Labium slightly wider than long. Sternum width and length nearly equal. Leg length commonly IV, I, II, III (I, IV, II, III in *H. sanjuanensis*). Distance from spiracle to spinnerets 0.3 to 0.9 times the distance from spiracle to epigastric furrow. Proximal segment of each lateral spinneret 1.5 to 2.5 times as long as distal segment.

Male palpus with femur and tarsus nearly equal in length, each nearly equal to the combined lengths of patella and tibia. Tibial apophysis distal and retrolateral, either gradually curved distally (*H. flaviceps, H. glacialis, H. nobilis, H. okefinokensis, H. sanjuanensis, H. veracruzana*) or directed distally and strongly recurved (*H. arizonica, H. cinerea, H. ononidum*). Patellar spur proximal and retrolateral, basal two-thirds straight and distal portion bent or hooked. Cymbium oval, slightly longer

than wide. Seminal canal clearly visible only in *H. flaviceps, H. glacialis, H. nobilis, H. okefinokensis, H. sanjuanensis,* and *H. veracruzana.* A tuft of setae forms a brush on the proximal, prolateral margin of the cymbium in *H. arizonica, H. cinerea,* and *H. ononidum.* The embolus arises at the mid-retrolateral margin of the cymbium and completes or nearly completes a circle around the cymbium.

Openings may be located in the anterior region of the epigynum (*H. flaviceps, H. glacialis, H. sanjuanensis*), in the center of the epigynum (*H. nobilis, H. okefinokensis*), or at the posterior of the epigynum (*H. arizonica, H. cinerea, H. ononidum*). Bulbs may be large (*H. arizonica, H. cinerea, H. ononidum*), very small (*H. sanjuanensis*), or absent (*H. flaviceps, H. glacialis, H. nobilis, H. okefinokensis*). *Hahnia flaviceps* and *H. sanjuanensis* have highly coiled ducts while those of other species are more simply arranged. Spermathecae of all species but *H. sanjuanensis* are large.

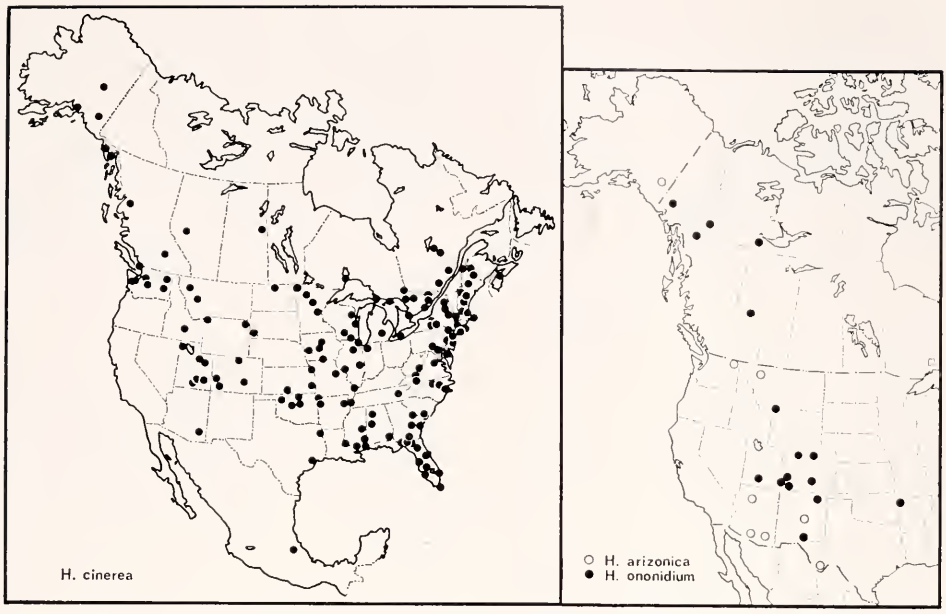
Key to the Male *Hahnia*

1 Tibial apophysis recurved; brush on proximal, prolateral portion of cymbium (Figs. 80, 81, 86, 87). 2
– Tibial apophysis straight or only slightly curved· no brush on cymbium (Figs. 104, 105, 112, 113). 4
2(1) Dorsum of abdomen without chevrons or with only very faint markings (Fig. 93); patellar spur bent, but not hooked (Figs. 91, 92). ..... *ononidum*
– Dorsum of abdomen with conspicuous chevrons (Figs. 82, 83, 88); patellar spur hooked (Figs. 80, 86). 3
3(2) Venter of abdomen with U-shaped white patch; proximal segment of lateral spinneret over twice as long as distal segment (Figs. 11, 80–83). ..... *cinerea*
– Venter of abdomen with one median and two lateral light stripes; proximal segment of lateral spinneret less than twice as long as distal segment (Figs. 86–88). ..... *arizonica*
4(1) Tibial apophysis twice as long as tibia (Figs. 97, 108, 112). 5
– Tibial apophysis as long as or shorter than tibia (Figs. 101, 104, 114). 7
5(4) Cymbium drawn out into a fingerlike distal extension; tibial apophysis nearly straight; patellar spur bifurcate at tip (Figs. 112, 113). ..... *flaviceps*
– Cymbium rounded at distal end; patellar spur with single point (Figs. 97, 108). 6
6(5) Tip of tibial apophysis curved retrolaterally, basal one-third of tibial apophysis about one-sixth width of tibia; two to four retromarginal teeth on each chelicera (Figs. 108, 109). ..... *glacialis*
– Tip of tibial apophysis bent prolaterally, basal one-third of tibial apophysis about one-half width of tibia; one retromarginal tooth on each chelicera (Figs. 97, 98). ..... *sanjuanensis*
7(4) Tibial apophysis one and one-third times as long as tibia (Figs. 114, 115); AME minute. ..... *veracruzana*
– Tibial apophysis one-third to two-thirds as long as tibia (Figs. 101, 104). 8
8(7) Dorsum of abdomen tan; tibial apophysis one-third as long as tibia (Figs. 104, 105); southern Georgia ..... *okefinokensis*
– Dorsum of abdomen gray with four light chevrons and four light ovals; tibial apophysis two-thirds as long as tibia (Figs. 101, 102); southern Mexico ..... *nobilis*

Key to the Female *Hahnia*

(Females of *H. veracruzana* are not known)

1 No bulbs present; short ducts lead from openings directly to spermathecae (Figs. 99, 100, 103); epigynum very indistinct, details visible only under high magnification after clearing. 2
– Bulbs present (Figs. 79, 85, 90) or absent (Figs. 96, 107, 111), if absent, long coiled ducts lead to spermathecae; epigynum distinct, some details visible under low magnification without clearing. 3
2(1) Ducts form a circle before entering spherical spermathecae medially (Figs. 99, 100); southern Mexico. ..... *nobilis*
– Ducts pass laterally to enter elongate spermathecae anteriorly (Fig. 103); southern Georgia. ..... *okefinokensis*
3(1) Openings in anterior third of epigynum (Figs. 95, 106, 110). 4
– Openings in posterior third of epigynum (Figs. 78, 84, 89). 6
4(3) Large distinct spermathecae about four times as wide as ducts; openings not encircled by ducts (Figs. 106, 107, 110, 111). 5
– Small indistinct spermathecae, appearing as knobs at the end of each duct, less than



Map 7. Distribution of *Hahnia cinerea* Emerton, *Hahnia arizonica* Chamberlin and Ivie, and *Hahnia ononidum* Simon.

two times as wide as ducts; openings encircled by anterior loops of ducts (Figs. 94–96). ..... *sanjuanensis*

5(4) Ducts highly coiled; spermathecae not contiguous (Figs. 110, 111). ..... *flaviceps*

– Ducts not highly coiled; spermathecae contiguous along most of their median surfaces (Figs. 106, 107). ..... *glacialis*

6(3) Bulbs ovate; ducts leaving their posterior median surfaces (Figs. 78, 79). ..... *cinerea*

– Bulbs elongate or comma-shaped; ducts leaving their posterior lateral or lateral margins (Figs. 84, 85, 89, 90). 7

7(6) Abdomen with conspicuous light chevrons (Fig. 88); bulbs separated by a distance equal to two-thirds their width, long axes of bulbs directed anterior-posteriorly (Figs. 84, 85). ..... *arizonica*

– Abdomen without conspicuous light chevrons (Fig. 93); bulbs nearly contiguous, their long axes directed laterally (Figs. 89, 90). ..... *ononidum*

Hahnia cinerea Emerton
Figures 11, 12, 78–83; Map 7

Hahnia cinerea Emerton, 1890, Trans. Conn. Acad. Arts Sci., 8: 197, pl. 7, figs. 9a, b. Male and three female syntypes from Swampscott, Massachusetts, in Museum of Comparative Zoology, examined.

Hahnia cinerea seminola Gertsch, 1934, Amer. Mus. Novitates, No. 712: 3, 8. Male holotype and four paratypes from Gainesville, Florida, in American Museum of Natural History, examined. NEW SYNONYMY.

Description. Total length about 2.00 mm, female generally larger than male. Legs banded, dorsum of abdomen with five to six chevrons (Figs. 82, 83). Carapace about 0.80 mm long and 0.64 mm wide. Eye ratio AME:ALE:PME:PLE = 1:2:1.5:2. Length and width of sternum 0.50 mm. Labium 0.08 mm long, 0.14 mm wide. Three to five nearly equal-sized retromarginal teeth on each chelicera. Abdomen 1.08 to 1.45 mm long. Distance from spiracle to spinnerets 0.5 times the distance from spiracle to epigastric furrow in male, 0.6 times in female. Proximal segment of lateral spinneret 1.8 times as long as distal segment in male, 1.6 times in female.

Diagnosis. A brush on the proximal, prolateral portion of the cymbium (Fig. 81), a recurved tibial apophysis, and a transparent conductor on the distal, prolateral surface of the cymbium (Fig. 80) dis-

tinguish this species from all other North American *Hahnia* except *H. arizonica* and *H. ononidum* with which it is sympatric in western North America. Males of *H. cinerea* and *H. arizonica* have conspicuous chevrons on the dorsum of the abdomen (Figs. 82, 83, 88) and a hooked patellar spur (Fig. 80), while those of *H. ononidum* have only very faint color markings on the abdomen (Fig. 93) and a bent patellar spur (Fig. 91). *Hahnia cinerea* has a median white patch on the venter of the abdomen while *H. arizonica* has three light median stripes. In *H. cinerea* the proximal segment of the lateral spinnerets is about 1.8 times as long as the distal segment, while in *H. arizonica* it is about 2.4 times as long.

Females of *H. cinerea* have the epigynal opening located anterior to the rear margin of the spermathecae (Fig. 79), while in *H. arizonica* (Fig. 85) and *H. ononidum* (Fig. 90) the openings are at the level of the rear margins of the spermathecae. The bulbs of *H. cinerea* are oval and much less elongate than the other species, and the ducts leading from the openings connect to their median surfaces rather than the lateral surfaces as in the *H. arizonica* and *H. ononidum*. *Hahnia cinerea* also differs from *H. ononidum* by having conspicuous chevrons on the dorsum of the abdomen.

Variation. Specimens collected from the Florida Keys north to eastern central Florida show more contrast in light and dark markings on the carapace, sternum, legs, and abdomen and have less symmetrical abdominal markings (Fig. 83) than specimens from elsewhere in North America (Fig. 82), as noted by Gertsch (1934). In specimens from Alachua Co., Columbia Co., Highlands Co., Monroe Co., Palm Beach Co., and Sarasota Co., all of which showed this color pattern, no clinal variation was apparent. Details of the epigynum and palp of these specimens are the same as other *H. cinerea* and other structural features fall within the range of those for specimens examined. At present it seems appropriate only to note this color difference and not to interpret it as defining the subspecies *H. cinerea seminola* as does Gertsch (1934).

Distribution. Nova Scotia south to the Florida Keys, southern Mexico, and Arizona, west to Arizona, Washington, and Alaska (Map 7).

Hahnia arizonica Chamberlin and Ivie

Figures 84–88; Map 7

Hahnia arizonica Chamberlin and Ivie, 1942, Bull. Univ. Utah, 32(13): 26, figs. 54, 55, ♂, ♀. Female holotype, seven male and 13 female paratypes from Oak Creek Canyon, 20 mi. S. of Flagstaff, Arizona, in American Museum of Natural History, 19 paratypes examined.

Description. Total length about 2.00 mm, females generally larger than males. Legs banded, dorsum of abdomen with six or seven light chevrons (Fig. 88). Carapace about 0.90 mm long and 0.72 mm wide. Eye ratio AME:ALE:PME:PLE = 1:2:2:2.3. Length and width of sternum 0.52 mm.

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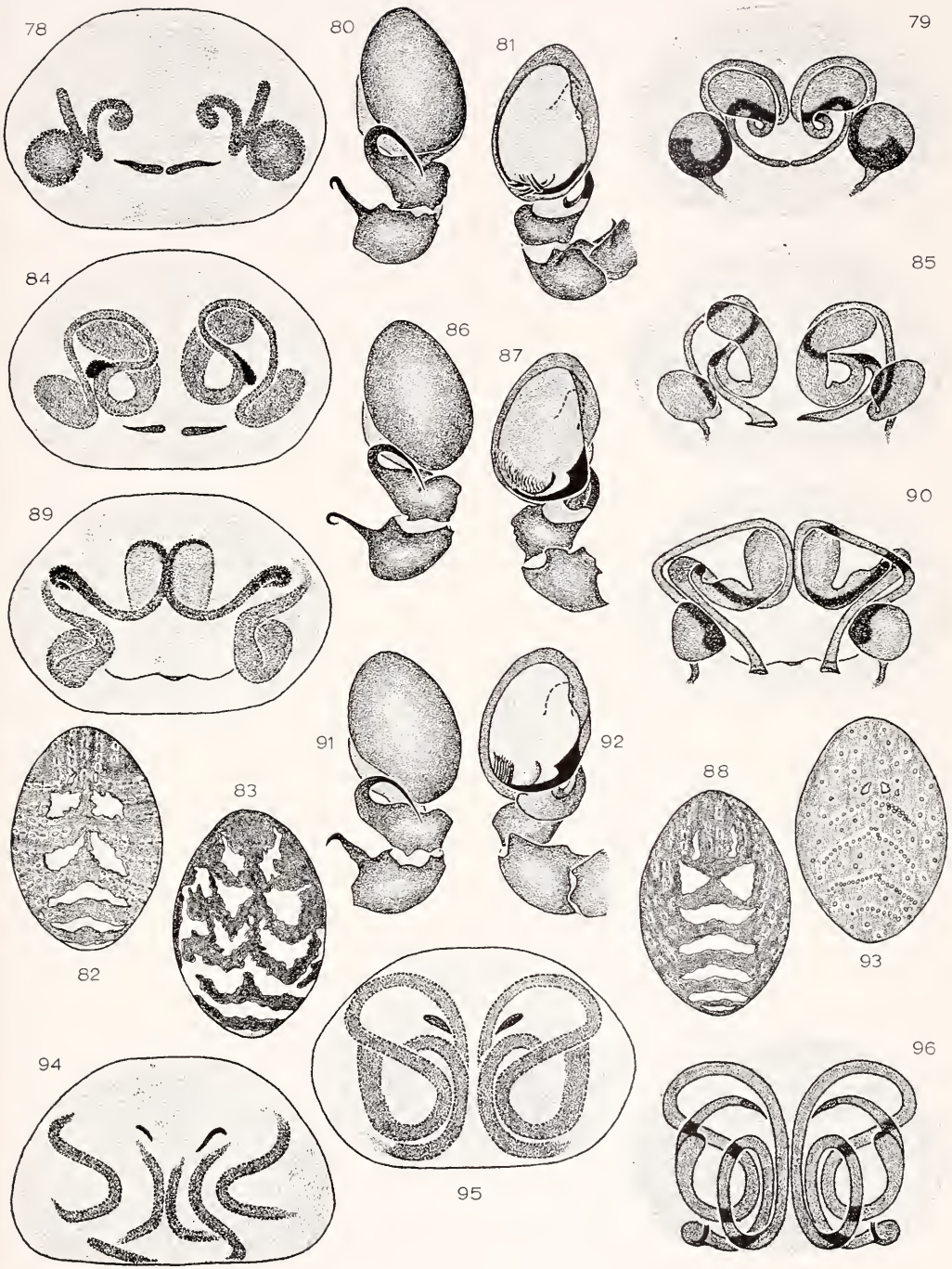
Figures 78–83. *Hahnia cinerea* Emerton. 78. Ventral view of epigynum. 79. Dorsal view of cleared epigynum. 80. Dorsal view of left male palpus. 81. Ventral view of left male palpus. 82. Dorsum of abdomen of male from New Jersey. 83. Dorsum of abdomen of male from Florida.

Figures 84–88. *Hahnia arizonica* Chamberlin and Ivie. 84. Ventral view of epigynum of paratype. 85. Dorsal view of cleared epigynum of paratype. 86. Dorsal view of left palpus of male paratype. 87. Ventral view of left palpus of male paratype. 88. Dorsum of abdomen of male from Arizona.

Figures 89–93. *Hahnia ononidum* Simon. 89. Ventral view of epigynum of paratype. 90. Dorsal view of cleared epigynum of paratype. 91. Dorsal view of left palpus of male paratype. 92. Ventral view of left palpus of male paratype. 93. Dorsum of abdomen of male from Wyoming.

Figures 94–96. *Hahnia sanjuanensis* Exline. 94. Ventral view of epigynum of holotype. 95. Ventral view of epigynum of female from California. 96. Dorsal view of cleared epigynum (95).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Labium 0.10 mm long and 0.17 mm wide. Four retromarginal teeth of nearly equal size on each chelicera. Abdomen 1.18 to 1.56 mm long. Distance from spiracle to spinnerets 0.4 times the distance from spiracle to epigastric furrow in male, 0.5 times in female. Proximal segment of lateral spinneret 2.4 times as long as distal segment in male and female.

Diagnosis. Males can be distinguished from those of *H. ononidum* by their conspicuous abdominal chevrons (Fig. 88) and by a hooked (Fig. 86) rather than a bent patellar spur. It is difficult to distinguish *H. arizonica* and *H. cinerea* males since both have similar color patterns and palps. The venter of *H. arizonica*'s abdomen is generally marked with three light median stripes, while *H. cinerea* has a median white patch. In *H. arizonica* the proximal segment of the lateral spinneret is about 2.4 times as long as the distal segment, while in *H. cinerea* it is about 1.8 times as long.

Females of *H. arizonica* have conspicuous chevrons on the abdomen which distinguish them from *H. ononidum*. *H. arizonica* females may be distinguished from both sympatric species, *H. cinerea* and *H. ononidum*, by having comma-shaped bulbs (Fig. 85) which are separated by at least two-thirds their width and have their long axes nearly parallel to, rather than perpendicular to, the median body plane.

Distribution. Southwestern Texas, west to Arizona, and north of Alaska (Map 7).

Hahnia ononidum Simon
Figures 89–93; Map 7

Hahnia ononidum Simon 1875, Arachnides de France, 2: 135–136. Male and female syntypes from the high Alps at Monétier-de-Briancon, France, in the Muséum National d'Histoire Naturelle, Paris, examined.

Hahnia inornata Chamberlin and Ivie, 1942, Bull. Univ. Utah, 32(13): 26–27, figs. 56, 57, ♂, ♀. Female holotype and three paratypes from Pine Springs, Henry Mtns., Utah, in American Museum of Natural History, examined. First synonymized by Lehtinen, 1967.

Description. Total length about 1.90 mm, females and males nearly equal in size. Legs only faintly banded, dorsum of abdomen without conspicuous chevrons (Fig. 93). Carapace about 0.80 mm long and 0.64 mm wide. Eye ratio AME:ALE:PME:PLE = 1:1.5:1.5:1.5. Length and width of sternum about 0.45 mm. Labium 0.08 mm long and 0.17 mm wide. Two to three retromarginal teeth on each chelicera. Abdomen 1.04 to 1.60 mm long. Distance from spiracle to spinnerets 0.4 times the distance from spiracle to epigastric furrow in male, 0.6 times in female. Proximal segment of lateral spinneret 3.0 times as long as distal segment in male, 2.0 times in female.

Diagnosis. Both males and females may be distinguished from their sibling species, *H. arizonica* and *H. cinerea*, by their very faint abdominal chevrons (Fig. 93).

The male palp has a patellar spur which is bent (Fig. 91), but not hooked as in the other two species. The female epigynum has elongate, comma-shaped bulbs with bursae connected to their lateral surfaces (Fig. 90) as does *H. arizonica*, but, unlike *H. arizonica*, the long axis of these bulbs is oriented perpendicular to the longitudinal axis of the body and the bulbs are not separated by more than one-fourth the width of each.

Discussion. Lehtinen (1967) treats *H. ononidum*, *H. cinerea*, and *H. inornata* as synonyms. Although *H. ononidum* and *H. inornata* are clearly synonyms, as indicated by similar color patterns and similar male and female genitalia, *H. cinerea* and *H. arizonica* appear to be closely related but distinct species.

Distribution. Southern New Mexico east to northwestern Arkansas, west to Utah, and north to southwestern Yukon (Map 7).

Hahnia sanjuanensis Exline
Figures 10, 94–98; Map 8

Hahnia sanjuanensis Exline, 1938, Univ. Wash. Publ. Biol., 9(1): 32, fig. 45, ♀. Female holotype from Friday Harbor, Washington, in American Museum of Natural History, examined.

Map 8. Distribution of *Hahnia sanjuanensis* Exline, *Hahnia nobilis* n. sp. (nobila, not correct, on map), *Hahnia okefinokensis* Chamberlin and Ivie, *Hahnia glacialis* Soerensen, *Hahnia flaviceps* Emerton, and *Hahnia veracruzana* Gertsch and Davis.

Hahnistea longipes Chamberlin and Ivie, 1942, Bull. Univ. Utah, 32(13): 27–28, fig. 58, ♀. Female holotype from Potter Creek Cave (W 123°: N 40°), California, in American Museum of Natural History, examined. First synonymized by Lehtinen, 1967.

Description. Total length 1.70 to 2.38 mm. Male tan, female with six to seven faint chevrons on dorsum of abdomen. Carapace about 0.70 mm in width and length. Eye ratio AME:ALE:PME:PLE = 1:2.5:2.5:2.5. Sternum 0.44 mm long and 0.53 mm wide. Labium 0.09 mm long, 0.16 mm wide. One small retromarginal tooth on each chelicera. Abdomen 1.00 to 1.79 mm long. Distance from spiracle to spinnerets 0.3 times the distance from spiracle to epigastric furrow in male, 0.6 times in female. Proximal segment of lateral spinneret 1.9 times as long as distal segment in male, 1.7 times in female.

Diagnosis. Males are similar to those of *H. flaviceps* and *H. glacialis,* all of which have a nearly straight tibial apophysis about twice as long as the tibia. *H. sanjuanensis* males may be separated from those of *H. flaviceps* by the presence of a rounded (Fig. 97) rather than a pointed (Fig. 112) cymbium tip and by the presence of a single-pointed rather than a double-pointed, patellar spur. The basal one-third of the tibial apophysis of *H. sanjuanensis* is about one-half as wide as the tibia (Fig. 97), while that of *H. glacialis* is about one-sixth as wide as the tibia (Fig. 108). Females are distinguished by oblique epigynal openings situated in the anterior one-third of the epigynum, separated by a distance equal to the width of each opening, and generally encircled by a loop of the duct (Figs. 94, 95). Bulbs and spermathecae are

much reduced and the ducts form several large loops (Fig. 96).

Discussion. The male described above is the first identified with this species and was collected from Spanish Fork Canyon, Utah Co., Utah, on 2 November 1951 by D. E. Beck. It is deposited in the American Museum of Natural History. Although not collected with a female, this specimen has the long, thin legs (the first longer than the rest) and reduced coloration characteristic of *H. sanjuanensis* females. Dimensions of the carapace, sternum, and labium as well as the position of the spiracle and relative length of the spinneret segments correspond to those of female specimens of *H. sanjuanensis.* Lehtinen (1967) recognized the synonymy of *Hahnia sanjuanensis* and *Hahnistea longipes,* but considered this species to be in the genus *Hahnistea.* As mentioned in the discussion of *Hahnia* the genus *Hahnistea* does not seem valid.

Distribution. Southeastern Arizona west to northern Baja California, north to north-central Utah and northwestern Washington (Map 8).

Hahnia nobilis n. sp.
Figures 99–102; Map 8

Types. Female holotype, three male and three female paratypes from five miles north of Encarnacion, Hidalgo, Mexico (W 99.12: N 20.55), collected 28 July 1966 by Jean and Wilton Ivie, in the American Museum of Natural History. The name of this species is derived from a Latin translation of the Mexican name of the state in which types were collected.

Description. Total length 1.5 mm. Legs and palps tan, dorsum of abdomen with four light chevrons in the posterior one-half and four light ovals in the anterior one-half. Cardiac muscle scars indistinct. Venter of male's abdomen tan, female with a wide, light, transverse stripe on venter of abdomen. Carapace 0.66 mm long and 0.48 mm wide. Eye ratio of male, AME:ALE: PME:PLE = 1:3.5:2.5:3.5, of female, 1:2.5: 2.5:2.5. Length and width of sternum 0.40 mm. Labium 0.08 mm long and 0.14 mm wide. Male with three and female with two retromarginal teeth on each chelicera. Abdomen 0.80 to 0.85 mm long. Distance from spiracle to spinnerets 0.4 times the distance from spiracle to epigastric furrow in male, 0.6 times in female. Proximal segment of lateral spinneret 1.8 times as long as distal segment in male, 1.6 times in female.

Diagnosis. Males of *H. nobilis* (Figs. 101, 102) are similar to those of *H. okefinokensis* (Figs. 104, 105) and *H. veracruzana* (Figs. 114, 115), all of which have a relatively short, straight tibial apophysis. In *H. nobilis* the tibial apophysis is two-thirds as long as the tibia, in *H. okefinokensis* one-third as long, and in *H. veracruzana* one and one-third times as long. *Hahnia nobilis* has light chevrons and ovals on the dorsum of its abdomen while *H. okefinokensis* does not. Females have a very small, simple epigynum (Figs. 99, 100) similar to that of *H. okefinokensis* (Fig. 103), but somewhat more distinct. In *H. nobilis* the ducts make a circle before connecting to the median surfaces of oval spermathecae; whereas, the short ducts of *H. okefinokensis* pass laterally to enter the anterior surfaces of elongate spermathecae.

Distribution. Known only from the type locality in southeastern Mexico (Map 8).

Hahnia okefinokensis Chamberlin and Ivie
Figures 103–105; Map 8

Hahnia okefinokensis Chamberlin and Ivie, 1934 in Gertsch, Amer. Mus. Novitates, No. 712: 8. Male holotype and two female paratypes from east side of Okefinokee Swamp, Georgia, collected 23 August 1933 by Wilton Ivie, in American Museum of Natural History, examined.

Unzickeria okefinokensis, – Lehtinen, 1967, Ann. Zoologici, 4: 199–496.

Note. There appear to be more paratypes than mentioned by Chamberlin and Ivie in the original species description. The authors examined one male and three female paratypes from the American Museum of Natural History, all collected by W. Ivie

on the date and from the locality mentioned above. The male examined was damaged so that it could not be accurately measured.

Description. Total length 1.68 mm. Legs tan, male and two females with dorsum of abdomen tan, one female with four light chevrons and two light ovals on the dorsum of gray abdomen. Carapace 0.67 mm long, 0.54 mm wide. Eye ratio AME:ALE:PME:PLE = 1:4:4:4. Length and width of sternum 0.40 mm. Labium 0.08 mm long, 0.13 mm wide. Two retromarginal teeth on each chelicera of female. Distance from spiracle to spinnerets 0.3 times the distance from spiracle to epigastric furrow in female. Proximal segment of lateral spinneret 1.7 times as long as distal segment in female.

Diagnosis. Males are similar to those of *H. nobilis* and *H. veracruzana,* all of which have a palp with a slightly curved apophysis which is less than half as long as the palpal tarsus. In *H. okefinokensis* (Figs. 104, 105) the tibial apophysis is one-third as long as the tibia, in *H. nobilis* (Figs. 101, 102) two-thirds as long, and in *H. veracruzana* (Figs. 114, 115) one and one-third times as long as the tibia. Details of the epigynum (Fig. 103), like those of *H. nobilis* (Figs. 99, 100), are very indistinct. While very few details can be seen through the uncleared epigynum of *H. nobilis,* this is not possible in *H. okefinokensis.* In *H. okefinokensis* the ducts pass laterally to enter the anterior surfaces of elongate spermathecae, while in *H. nobilis* the ducts form a circle before entering the median margins of oval spermathecae.

Distribution. Known only from the type locality in southeastern Georgia (Map 8).

Hahnia glacialis Soerensen
Figures 106–109; Map 8

Hahnia glacialis Soerensen, 1898, Vid. Medd. Natur. Foren. Kjöbenh., 1898: 219. Type locality Greenland, type specimens in Copenhagen Museum, examined.

Hahnia monticola Bryant, 1941, Psyche, 48(4): 132–134, fig. 1, ♀. Female holotype and paratype from Mt. Washington, New Hampshire, in Museum of Comparative Zoology, examined. NEW SYNONYMY.

Description. Total length 2.35 mm. Legs tan, dorsum of abdomen with six light chevrons. Carapace 0.94 mm long, 0.70 mm wide. Eye ratio AME:ALE:PME:PLE = 1:1.5:1.5:1.5. Length and width of sternum 0.56 mm. Labium 0.10 mm long, 0.16 mm wide. Two to four very small retromarginal teeth on each chelicera. Abdomen 1.37 to 1.60 mm long. Distance from spiracle to spinnerets 0.4 times the distance from spiracle to epigastric furrow. Proximal segment of lateral spinnerets 1.3 times as long as distal segment in male, 2.2 times in female.

Diagnosis. Hahnia glacialis males (Figs. 108, 109) are distinguished from all others except *H. flaviceps* and *H. sanjuanensis* by a long, straight tibial apophysis which is nearly as long as the tarsus. *Hahnia glacialis* differs from *H. flaviceps* (Figs. 112, 113) by having a palp whose tarsus is rounded distally rather than drawn to a point, and by having a single-pointed rather than a forked patellar spur. The basal one-third of the tibial apophysis in *H. glacialis* is one-sixth as wide as the tibia, while in *H. sanjuanensis* (Figs. 97, 98) it is one-half as wide as the tibia. Females of *H. glacialis* are distinguished by the pattern of their epigynum (Figs. 106, 107). The epigyneal openings are located in the anterior one-fourth of the epigynum, just anterior to the spermathecae. The spermathecae are large, elongate, contiguous along their median surfaces, and clearly visible in an intact epigynum. Lateral to each spermathecae is a semicircular loop of the duct with its open side directed posteriorly and laterally.

Discussion. Several specimens from Greenland were examined. This species has a very distinctive epigynum and male palp, so that illustrations and descriptions clearly establish its identity. Lehtinen (1967) places both *H. glacialis* and *H. monticola* in the genus *Neoantistea,* but retains them as separate species. Specimens examined clearly show that *H. glacialis* and *H. monticola* are synonyms and that this species should be kept in the genus *Hahnia*

as the arrangement of the spiracle, spinnerets, and eyes is characteristic of *Hahnia* and not *Neoantistea*.

Distribution. This boreal species is found from Alaska and the Yukon south to Colorado and southeast to northern New York and New Hampshire (Map 8).

Hahnia flaviceps Emerton
Figures 110–113; Map 8

Hahnia flaviceps Emerton, 1913, Bull. Amer. Mus. Nat. Hist., 32: 257. Male and female syntypes from swamp near railroad at Farmingdale, New Jersey, in American Museum of Natural History, examined.

Description. Total length 1.68 to 2.36 mm, females larger than males. Legs tan or with faint bands, abdomen with five or six light chevrons. Carapace 0.80 mm long, 0.60 mm wide. Eye ratio AME:ALE:PME:PLE = 1:2:2:2. Clypeus longer than any other North American member of the family, easily visible anterior to AME. Length and width of sternum 0.45 mm. Labium 0.08 mm long, 0.13 mm wide. Each chelicera with three nearly equal retromarginal teeth. Abdomen 0.84 to 1.31 mm long. Distance from spiracle to spinnerets 0.8 times the distance from spiracle to epigastric furrow in male, 0.9 times in female. Proximal segment of lateral spinnerets 1.5 times as long as distal segment.

Diagnosis. Males of *H. flaviceps* (Figs. 112, 113) are separated from all North American *Hahnia* except *H. glacialis* and *H. sanjuanensis* by a long, straight tibial apophysis which is nearly as long as the tarsus. The tarsus of *H. flaviceps* is drawn to a point distally while those of *H. glacialis* (Figs. 108, 109) and *H. sanjuanensis* (Figs. 97, 98) are rounded distally. *Hahnia flaviceps* is the only North American species of the genus with a double-pointed patellar spur. Females of *H. flaviceps* have epigyneal openings in the anterior one-third of the epigynum, medial to spirals of the ducts (Figs. 110, 111). Bursae connect directly to these ducts and there are no bulbs. Ducts are highly convoluted and lead to elongate spermathecae which do not show through an uncleared epigynum and are not contiguous along the midline of the epigynum.

Discussion. The long, highly-coiled ducts and absence of bulbs in the female epigynum, the extension of the tarsus of the male palp to a distal point, a long, sloping clypeus, and the location of the spiracle nearly midway between the base of median spinnerets and the epigastric furrow indicate that this species may not be closely related to any other North American *Hahnia*. However, *Hahnia* appears to be a more diverse genus than *Antistea* or *Neoantistea* and at present there appears no basis for treating it as other than a single genus.

Distribution. Indiana east to New Jersey

→

Figures 97–98. *Hahnia sanjuanensis* Exline. 97. Dorsal view of left male palpus. 98. Ventral view of left male palpus.

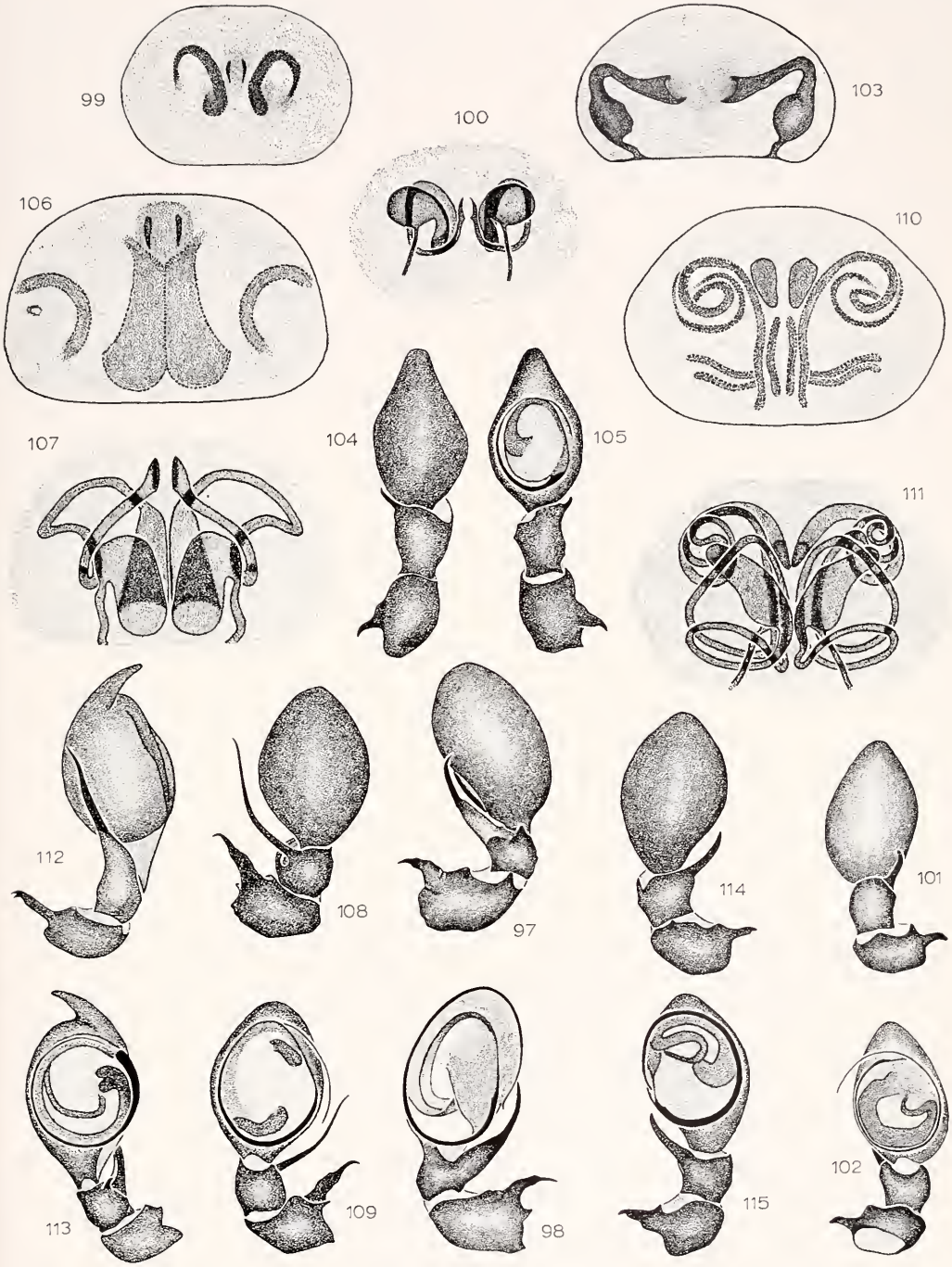
Figures 99–102. *Hahnia nobilis* n. sp. 99. Ventral view of epigynum of holotype. 100. Dorsal view of cleared epigynum of holotype. 101. Dorsal view of left palpus of male paratype. 102. Ventral view of left palpus of male paratype.

Figures 103–105. *Hahnia okefinokensis* Chamberlin and Ivie. 103. Dorsal view of cleared epigynum of paratype. 104. Dorsal view of left palpus of male paratype. 105. Ventral view of left palpus of male paratype.

Figures 106–109. *Hahnia glacialis* Soerensen. 106. Ventral view of epigynum. 107. Dorsal view of cleared epigynum. 108. Dorsal view of left male palpus. 109. Ventral view of left male palpus.

Figures 110–113. *Hahnia flaviceps* Emerton. 110. Ventral view of epigynum. 111. Dorsal view of cleared epigynum. 112. Dorsal view of left male palpus. 113. Ventral view of left male palpus.

Figures 114–115. *Hahnia veracruzana* Gertsch and Davis. 114. Dorsal view of right palpus of male holotype. 115. Ventral view of right palpus of male holotype.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and North Carolina, south to Mississippi and southeastern Texas (Map 8).

Hahnia veracruzana Gertsch and Davis
Figures 114–115; Map 8

Hahnia veracruzana Gertsch and Davis, 1940, Amer. Mus. Novitates, No. 1059: 14–15, fig. 20, ♂. Male holotype and male paratype from 15 mi. W. of Jalapa, Veracruz, Mexico, in American Museum of Natural History, examined.

Neohahnia veracruzana: – Lehtinen, 1967, Ann. Zoologici, 4: 199–496.

Description. Total length of male (females not known) 1.17 mm. Legs tan, dorsum of abodmen with five very faint chevrons. Carapace 0.54 mm long, 0.42 mm wide. Eye ratio AME:ALE:PME:PLE = 1:4:4:4, AME minute. Length and width of sternum 0.32 mm. Labium 0.03 mm long, 0.08 mm wide. Each chelicera with two very small, equal retromarginal teeth. Distance from spiracle to spinnerets 0.3 times the distance from spiracle to epigastric furrow. Proximal segment of lateral spinnerets of male 1.5 times as long as distal segment.

Diagnosis. Males are distinguished from all others of the genus except *H. nobilis* and *H. okefinokensis* by a slightly curved tibial apophysis which is less than half as long as the tarsus. *H. veracruzana* has a tibial apophysis which is one and one-third times as long as the tibia (Figs. 114, 115) while that of *H. nobilis* is two-thirds as long as the tibia (Figs. 101, 102) and that of *H. okefinokensis* is one-third as long as the tibia (Figs. 104, 105).

Distribution. Known only from the type locality in southeastern Mexico (Map 8).

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Systematics and Biogeography of the Tyrannid Genus *Todirostrum* and Related Genera (Aves)

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SYSTEMATICS AND BIOGEOGRAPHY OF THE TYRANNID GENUS *TODIROSTRUM* AND RELATED GENERA (AVES)

JOHN W. FITZPATRICK[1]

ABSTRACT. Of 32 Tody-tyrant species (family Tyrannidae), 14 comprise the genus *Todirostrum* and 12 are currently placed within *Idioptilon*. The remaining species represent six monotypic genera. *Todirostrum* species fall into two major species groups (labelled *cinereum* and *sylvia*), and the affinities of one additional, relict species (*capitale*) lie outside the genus. The distributional history of each species group can be approximately traced from the isolation of two ancestral populations. Alternating contraction and expansion of lowland South American forests, corresponding with dry and humid climatic phases, generated new species within each lineage. Their modern compositions and distribution patterns were determined by dispersal ability and competitive interactions between related species. Current distributions and plumage patterns appear to reflect the history of this radiation within *Todirostrum*.

Two relict species groups (one includes *T. capitale*, the other is an intermediate assemblage between *Todirostrum* and *Idioptilon* placed in the latter genus) illustrate the potential fate of many taxa in the rapidly radiating South American avifauna. As the number of species increases with cyclic production of new forms within lowland forest refuges, each faces increasing competitive pressure as it disperses. Certain species and whole lineages may be secondarily contracted into local distributions by dispersing, competitively superior relatives. The process culminates either in morphologic and ecological divergence by the inferior population, or in its eventual extinction. Intermediate stages in this "continental taxon cycle" are found in the Tyrannid group examined here.

Four specific taxonomic suggestions are offered in addition to comments on affinities within *Todirostrum*: 1) the genus *Ceratotriccus* should be merged with *Idioptilon*; 2) the genera *Taeniotriccus* and *Poecilotriccus* should be moved to positions immediately preceding that of *Todirostrum*, reflecting their affinities with *Todirostrum capitale*; 3) *Todirostrum* and *Idioptilon* should continue to stand as separate genera; 4) the genera *Microcochlearius* and *Snethlagea* are best merged with *Idioptilon*, while *Oncostoma* should continue to be generically recognized. A phylogeny of the Tody-tyrants and a revised classification of the group are proposed (Figure 4 and Table 1, respectively).

INTRODUCTION

Large complexes of closely related, often morphologically similar species are common in the diverse avifauna of South America. A number of recent studies have focused on ecological relationships between sympatric members of potentially competing species complexes (some examples in Cody, 1974). However, the evolutionary history behind modern distributions and ecological interactions is disregarded in many such studies, at the expense of an adequate perspective on the problems examined. The aim of the present study is to reconstruct this evolutionary background for a widely sympatric group of tropical, insectivorous bird species.

The Tyrannid subfamily Euscarthminae (Hellmayr, 1926) contains roughly 65 species, all of which are small and wholly insectivorous. This subfamily forms one of the four major phylogenetic lineages of small Tyrannidae (Smith, 1970), as shown in Figure 1. The core of the subfamily consists of an assemblage of 32 broad-billed species, placed in 10 genera by de Schauen-

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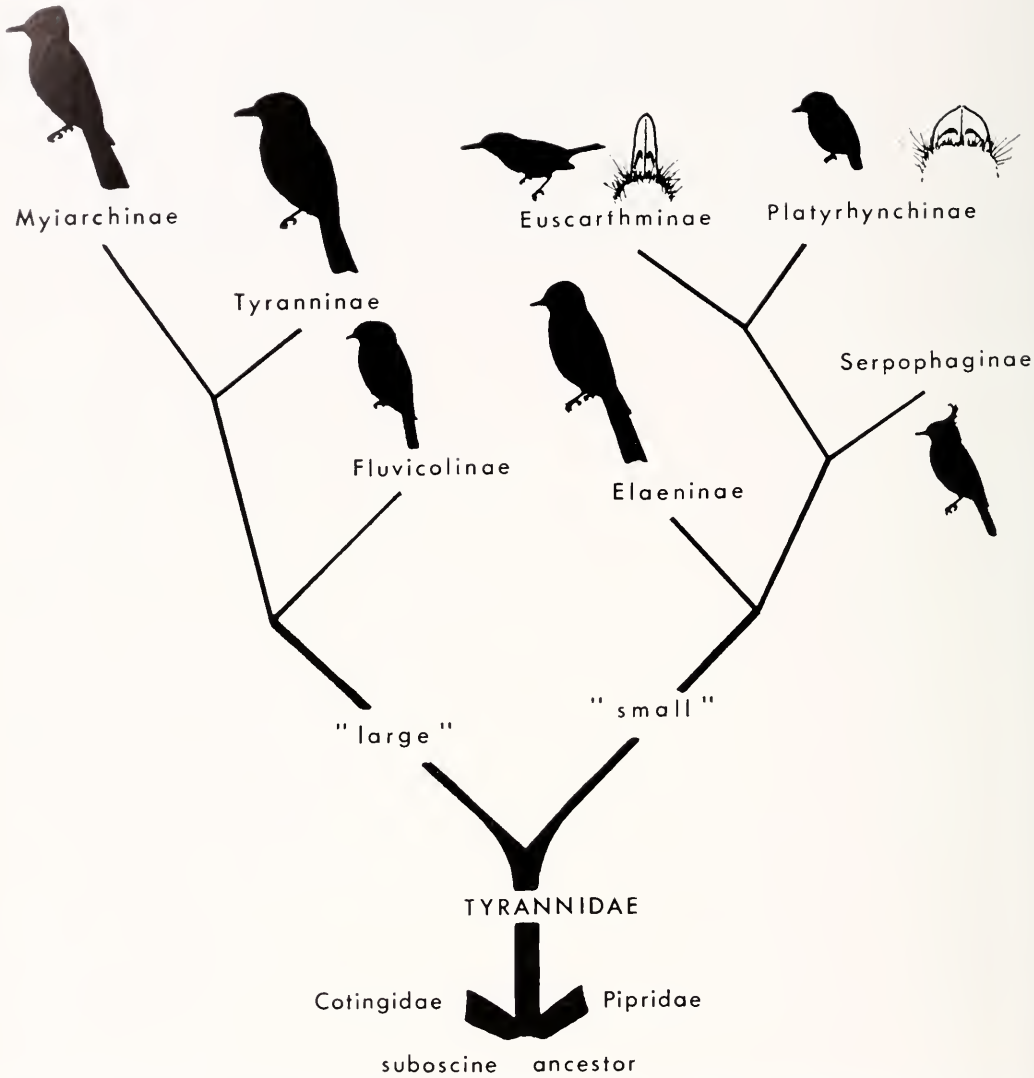

Figure 1. Schematic phylogeny of the family Tyrannidae, showing postulated relationships of the Euscarthminae within the "small" lineage. The seven subfamilies shown are those of Hellmayr (1926). Adapted from W. J. Smith (1970).

see (1966). The genera *Todirostrum* and *Idioptilon* contain 26 of these species (14 and 12 respectively), and each of the remaining 6 species is currently placed in a monotypic genus. Together, the 32 species clearly represent a well-circumscribed, monophyletic group, though their affinities have received little critical attention, and none at all since Zimmer's brief comments on some of them (1940, 1953, 1955).

As an initial stage in the investigation of the evolution and modern competitive structure of the group, the distributions of all Euscarthmine species were carefully plotted on maps. These distributions were examined in relation to recent theories in

South American biogeography. It became apparent that the patterns of radiation within several subgroups could be traced with reference to Pleistocene climate and vegetation fluctuations, the occurrence of which has been convincingly demonstrated by Haffer (1969, 1974) and Vanzolini and Williams (1970).

Distributional and morpholigic data relevant to two particular topics are presented in this paper: 1) A detailed description of speciation patterns in the genus *Todirostrum* is given. The account includes discussion of three related species heretofore placed in the monotypic genera *Poecilotriccus, Taeniotriccus,* and *Ceratotriccus,* and four additional species in the genus *Idioptilon.* 2) Certain general implications of the findings to modern biogeographic theory are discussed as they relate to the evolutionary history of certain members of the Euscarthmine assemblage.

Ultimately, the goals of present and forthcoming studies are to determine, 1) the modes of ecological and morphological radiation in this large group of similar, insectivorous species, 2) the varying competitive pressures placed on each other by such closely related forms, and 3) the ways in which various populations selectively respond to these pressures. Such analyses clearly depend upon establishing an evolutionary perspective with which to view modern geographical and ecological conditions. The present study is a first step, therefore, in that it focuses primarily upon the phylogenetic affinities within a subset of the Euscarthminae, and secondarily upon certain ecological implications. A brief discussion of taxonomic considerations germane to this analysis precedes the historical reconstruction of speciation in *Todirostrum.*

TAXONOMIC COMMENTS

Division of distinct morphologic groups into numerous, often monotypic genera was the rule during the early twentieth century classification of the Tyrannidae (e.g., Hellmayr, 1926). With several exceptions this early taxonomy has escaped revision within the subfamily Euscarthminae. It is now possible to assess the validity of certain of these genera. Specimens of all but two of the 32 Euscarthmine species in the Tody-tyrant lineage were assembled and examined in conjunction with the present study. The following comments and suggestions are based largely on morphologic patterns and biogeographic considerations covered later.

The species considered in this treatment of the genus *Todirostrum* Lesson, 1831 are those listed by de Schauensee (1966) with the following three exceptions: 1) *T. pictum* is considered to be one of three members of the *chrysocrotaphum* superspecies, as discussed in detail in the speciation section. It should therefore be listed as an allospecies along with *nigriceps* and *chrysocrotaphum.* 2) *T. hypospodium* Berlepsch, 1907 is considered a synonym of *T. sylvia superciliare* Lawrence, 1871. Known from a single unsexed specimen from the Bogotá trade market, *hypospodium* was listed as "a very doubtful species" by de Schauensee (1966: 365). Both Zimmer (1955) and Hellmayr (1926: 308) considered it a dark individual variant of *T. sylvia superciliare,* a fairly common species in the Magdalena Valley near Bogotá. The unlikely event of *hypospodium*'s proven validity as a species would have little bearing on the patterns discussed in this paper. 3) *T. albifacies* Blake, 1959 is considered conspecific with *T. capitale tricolor* (Berla, 1946). Blake (1959) listed the sex of the type (the only specimen collected to date) as uncertain, possibly male. Its close similarity to the female of sexually dimorphic *T. c. capitale* has led Blake and Traylor (personal communication) to reidentify it as a female *tricolor.* The latter form was heretofore known from a single type—unequivocally male—from the Rio Madeira, about 200 km downstream in the same drainage as the type locality of "*albifacies*" (see Fig. 10). Having examined the type of *albifacies* and the photographs in Berla's (1946) description of the male *tricolor,* I

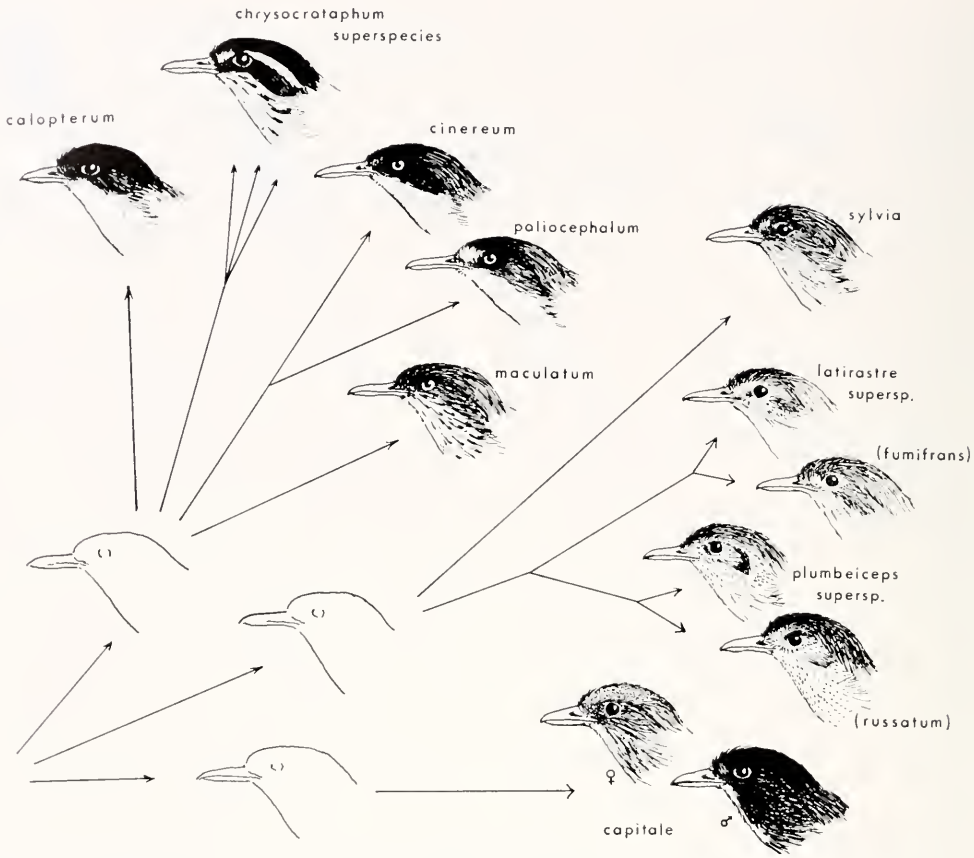

Figure 2. Head patterns in the three species groups making up the genus *Todirostrum*. Eleven of fourteen species are illustrated. Dotting about the faces in the *sylvia* group represents buffy plumage; lighter dots represent yellow plumage in the *cinereum* group; the crown of *capitale* female is dark rufous.

consider their similarities to nominate *capitale* sufficient to agree with Zimmer (1955) in treating the two populations as subspecies.

The 14 species in *Todirostrum* fall into three distinct species groups on the basis of bill characteristics and plumage patterns (Fig. 2). The *cinereum* group consists of four distinct species—*calopterum, cinereum, poliocephalum,* and *maculatum*—and an assemblage of three populations comprising the *chrysocrotaphum* superspecies: *chrysocrotaphum, nigriceps,* and *pictum*. Each of these seven forms has bright yellow underparts and a dark grey or solid black crown. Back color varies from rich green (in *chrysocrotaphum, maculatum,* and nominate *calopterum*) to grey or grey-green (*cinereum* and *poliocephalum*) to solid black (the isolated Peruvian race of *calopterum*). Throughout its range *maculatum* has numerous thin, brown streaks superimposed on its yellow breast and belly. Thick, solid black streaks form whole or partial necklaces in two members of the *chrysocrotaphum* superspecies. All other forms in this species group are clear-breasted. The progenitor for the species group is therefore assumed to have been a clear-breasted form—an assumption that will be used in reconstructing several speciation sequences to follow.

Six species are included here in the *sylvia* species group, though the affinities of *T. senex* remain in doubt. All have grey crowns and light grey underparts, lightening into white or pale yellow on the belly and undertail coverts. Backs of all species are dull green except for that of the southern Venezuelan endemic *russatum*, which has become dark olive-brown. The species group consists of one rather distinct, polytypic species, *T. sylvia*, and five (including *senex*) morphologically similar, allopatric populations here referred to collectively as the "*latirostre* complex." Important plumage differences occur in the amount of buffy or cinnamon coloration in the face and throat, almost entirely lacking in *sylvia* (Fig. 2). The bill of *sylvia* is basally wider than in the *latirostre* complex, and its breast and flanks show more uniform grey than in any of the other species. The extreme similarity between *plumbeiceps* and *russatum* is unequivocal (Zimmer, 1940). I agree with Mayr and Phelps (1967) in considering the latter to be a darkened, Roraiman counterpart of *plumbeiceps*, which is recognized here by placing both within the *plumbeiceps* superspecies. For the present I place *senex* in this group as well, on the basis of its buffy facial and throat plumage (Hellmayr, 1910).

The similarity between patterns of *T. fumifrons* and *T. latirostre*, especially the southeastern populations of the latter, is equivalent to that in the previous superspecies. They are clearly closer to each other than is either species to the *plumbeiceps* superspecies. Particularly considering the parapatry between *latirostre* and *fumifrons* along the Amazon (Fig. 9) it seems appropriate to treat these two as members of a second superspecies (*latirostre*) within the *latirostre* complex.

Todirostrum capitale stands apart from the remaining members of the genus. Its extremely wide bill is shared only by *senex* (Hellmayr, 1926: 309), a species that does not otherwise appear closely related. The plumage of *capitale* differs from that of all its congeners (partially illustrated in Fig. 2). The male is entirely black above with a white breast and belly, while the female is rich green above with a rufous crown, pearly-grey face and flanks, and white underparts washed with pale yellow under the tail. This pronounced sexual dimorphism is not only unique in the genus, but is quite rare in the entire family Tyrannidae. *T. capitale* stands as an aberrant member of *Todirostrum*, and actually appears to have closer affinities with two species—*Poecilotriccus ruficeps* and *Taeniotriccus andrei*—heretofore placed rather far from it within the Euscarthminae.

The monotypic genus *Poecilotriccus* was originally split from *Todirostrum* on the basis of the bushy rufous crown, relatively shorter bill, and somewhat shortened outer primaries of *ruficeps* (Ridgway, 1907). However, in basic plumage pattern *ruficeps* is remarkably similar to the female of *T. capitale* (see Fig. 3), and *capitale* shows the same short outer remiges. Besides its darkened male plumage, *capitale* differs from *ruficeps* only in its uniquely wide bill and much paler underparts. In general shape the bill of *ruficeps* (Fig. 3) closely approximates those of most other *Todirostrum* species.

Taeniotriccus andrei, a rare species in collections, is divergent from all other Euscarthmine species, especially in its deep, heavy bill. A number of striking similarities it shares with both *capitale* and *ruficeps*, however, provide virtually conclusive evidence for the close relationships among these three species: 1) *T. andrei* is sexually dimorphic; like *capitale*, the males are almost wholly black while females show more olive above (Fig. 3). 2) The bushy, deep rufous crown in both sexes of *andrei*, though interrupted in the center by a black crest, matches exactly the crown color of both *ruficeps* and *capitale* females. 3) Plumage patterns on the underparts of all three species are extremely similar, and resemble no other Euscarthmine species.

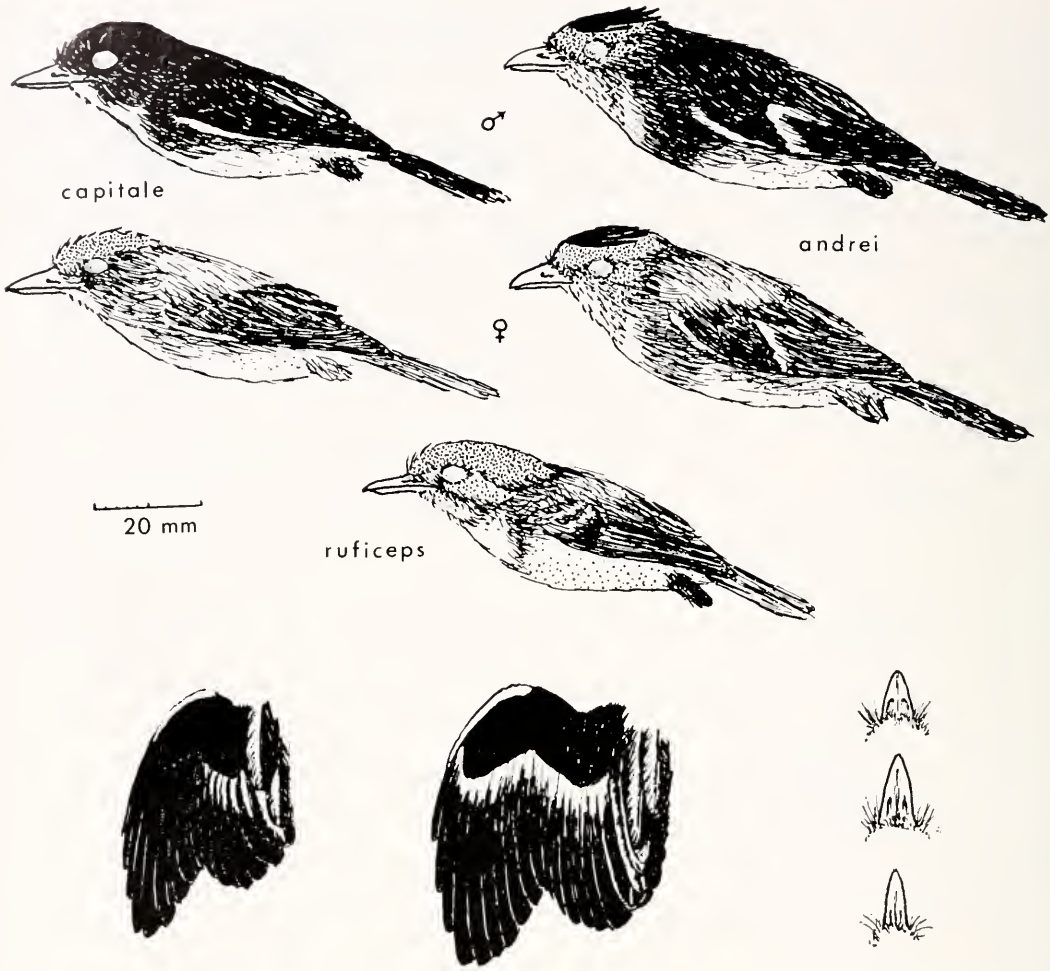

Figure 3. Plumage patterns and bill shapes of species comprising the *Todirostrum capitale* lineage. Both *capitale* and *Taeniotriccus andrei* are sexually dimorphic. Crowns of all but male *capitale* are rich rufous (heavy dots). Yellow on the breast (light dots) is most pronounced in *Poecilotriccus ruficeps*, but present in all forms. The hidden white stripe in the wing of *capitale* males (left) further reflects the probable affinities of this species with *andrei* (right). The bill of *ruficeps* (bottom) approaches the typical *Todirostrum* shape most closely, while the much heavier bills of *capitale* (middle) and *andrei* (top) have diverged considerably from those of all other Euscarthmine species. This may be associated with their long isolation as relict species within their rapidly diversifying tyrannid lineage.

The throat of *andrei* is light tawny, fading through light grey into a wash of yellow on the belly, but broken by a broad, black pectoral band. This pattern is precisely repeated in *ruficeps*, though the breast band is rather faint and the yellow below quite rich. Furthermore, nominate *capitale* shows a broken black breast band, and the relict form to the south even retains a complete one (Figure in Berla, 1946). 4) The striking yellow wing stripe in *andrei* appears at the outset to be unique, but even this character is present, if reduced, in *capitale;* the outer webbings of *capitale* specimens' innermost remiges are broadly edged with yellow. When the full wing

is opened, however, yellow bases on additional remiges are revealed, appearing even in the second and third secondaries in some specimens. This hidden yellow band corresponds exactly with the conspicuous wing pattern of *andrei* (see Fig. 3). 5) All three species have black thighs, which are absent in all remaining Euscarthmine species. All also have pale tarsi, though this character is not unique to these three forms. 6) In addition to these morphologic comparisons, biogeographic peculiarities indicate that all three species are secondarily restricted in their distributions (Fig. 10). In sum, the evidence strongly indicates that these species represent relicts from a single, ancestral divergence from a *Todirostrum* precursor.

Affinities among the three species are closer than those between the lineage as a whole and *Todirostrum* or *Idioptilon*. For this reason the current taxonomic positions of the three species are open to question. Possibly, they should be placed together in a separate genus from *Todirostrum*. While it seems the likely course at present, additional behavioral and anatomical study is required before effecting this rather major taxonomic shift. For the present, therefore, it seems sufficient to place the relict genera *Poecilotriccus* Berlepsch, 1884 and *Taeniotriccus* Berlepsch and Hartert, 1902 immediately before *Todirostrum* in a linear arrangement of the Tyrannidae, and to begin *Todirostrum* with the primitive species *capitale*.

Species in the genus *Idioptilon* Berlepsch, 1907 separate into two distinct plumage types, referred to here as the "brown" and "green" assemblages. The "brown" species group will be dealt with briefly in the speciation analyses to follow, as it appears to be rather closely related to *Todirostrum*. The five members of this group are "*Ceratotriccus furcatus*," *Idioptilon rufigulare*, *I. mirandae*, *I. kaemferi*, and *I. granadense*. They share conspicuously buffy eye-rings, tawny brown facial and throat plumage (darkened into a black throat in *granadense*), light olive backs, and relatively long tails. *Ceratotriccus furcatus* is a rare, isolated species, restricted to the coastal highlands of southeastern Brazil. Morphologically similar in most respects to the other "brown" species, *furcatus* was originally placed in its own genus on the basis of the lengthened outer rectrices, which result in a somewhat forked tail. While slightly wider distally than in most *Idioptilon* species, the relatively short bill of *furcatus* shows a close affinity to that genus, despite its original description as "*Todirostrum furcatum*." The clear morphologic similarities it shares with the other four members of the "brown" species group are supplemented by biogeographic considerations; all species, including *furcatus*, are secondarily restricted in their distributions (Fig. 11, discussion in *Idioptilon* section).

Recognizing *furcatus* as one of the representatives in a single lineage, the other members of which are all in the genus *Idioptilon*, it seems appropriate at this time to consider it a member of that genus. I propose, therefore, that *Ceratotriccus* Cabanis, 1874 be merged with *Idioptilon* Berlepsch, 1907, and that the species henceforth be recognized as *Idioptilon furcatum* (Lafresnaye, 1846).

Idioptilon kaemferi is included as a race of *I. mirandae* by de Schauensee (1966), even though both Zimmer (1953) and Eisenmann (in de Schauensee, 1966: 366) consider it specifically distinct. The forms are undoubtedly close relatives (specimens of both species examined), but they occur in very local distributions in eastern Brazil separated from each other by more than 2,000 km. Until further information can be obtained, they should be recognized as distinct, and are treated here as members of the *mirandae* superspecies.

Todirostrum senex (known only from the type specimen, stored in the Vienna Museum) may actually be another in this group of relict species, rather than a member of the *plumbeiceps* superspecies as previously speculated. This is suggested by its very rusty face and throat as well as its

exceeding rarity. Its unique bill, however, is wider than that of any modern *Idioptilon* species, and the hypothesis cannot be further examined until the type can be compared critically with the other representatives of the relict species group.

The hypothesis that the "brown" *Idioptilon* assemblage comprises a primitive lineage is supported by the species' distinct similarities to certain members of the genus *Todirostrum*. In overall plumage pattern, and particularly in bill shape, the "brown" group contains species that are morphologically intermediate between typical ("green") *Idioptilon* species and those in the *Todirostrum latirostre* complex. *T. plumbeiceps* and *T. russatum* were, in fact, originally placed in the genus "*Euscarthmornis*," which was later synonymized with *Idioptilon*. Before the transfer of these species into *Todirostrum* (Zimmer, 1940), Hellmayr (1926: 317) had written that (*Idioptilon*) *rufigulare* was nearest to *Euscarthmornis plumbeiceps*. Furthermore, *Idioptilon mirandae* was originally placed in the genus *Todirostrum* (Snethlage, 1925). Hellmayr (1926: 305) compared it most closely with *Todirostrum fumifrons*, but noted that it "provides the passage to *Euscarthmornis*."

The *latirostre* complex and the "brown" *Idioptilon* species group may actually reflect a morphologic pattern carried by an ancestral form which was to give rise to the entire *Todirostrum* and *Idioptilon* lineages. Their current similarity would thus have resulted from each conserving certain characters in their common ancestry.

Despite the existence of clearly intermediate forms, the generic separation of *Todirostrum* and *Idioptilon*, questioned by de Schauensee (1970), Short (1975), W. J. Smith (personal communication) and others, should be retained for the present. The separation prevents informative superspecies and species group divisions from being buried in nomenclature. Additional information, particularly regarding display behavior and vocalizations of most species, is necessary before the validity of this division can be more accurately reassessed.

More typical *Idioptilon* species comprise the "green" assemblage, to which subgroup *Microcochlearius josephinae*, *Snethlagea minor*, and *Oncostoma cinerigulare* are closely related. *Oncostoma*—the Bentbill—represents a rather divergent Central American offshoot from *Idioptilon*, and its generic separation appears to be warranted. Smith (in a letter) concurs on the basis of the unique vocalizations of this form in Panama. The first two monotypic genera, on the other hand, are clear continental representatives of the "green" assemblage. Both were separated early in this century on the basis of minor variations from the basic *Idioptilon* bill structure. *M. josephinae* has an excessively wide bill, and *S. minor* shows peculiarly circular, exposed nostrils in many specimens. In all other characters, however, they precisely match those of the "green" *Idioptilon* species group. Recognizing their phyletic positions within one subgroup of a larger, generically recognized taxon, I prefer to merge *Microcochlearius* Chubb, 1919 and *Snethlagea* Berlepsch, 1909 with *Idioptilon* Berlepsch, 1907. Affinities of *josephinae* remain in some doubt, but it appears certain that *minor* is closest to *I. spodiops* and *I. zosterops* within this species group, based on similarities between the bill and nostril structures in these three species. Little attention is given here to the biogeography of the "green" assemblage, pending field studies of most species.

In order to summarize the phylogenetic affinities within it, a diagram of the entire Tody-tyrant lineage as commented upon in this paper is shown here as Figure 4. While additional behavioral and anatomical data may modify it slightly, the gross relationships indicated are defendable at this time. Phyletic relationships are considered in this paper primarily as a step toward elucidating some biogeographic implications of Tyrannid distributions. Still, when such a synthesis is possible, it should be

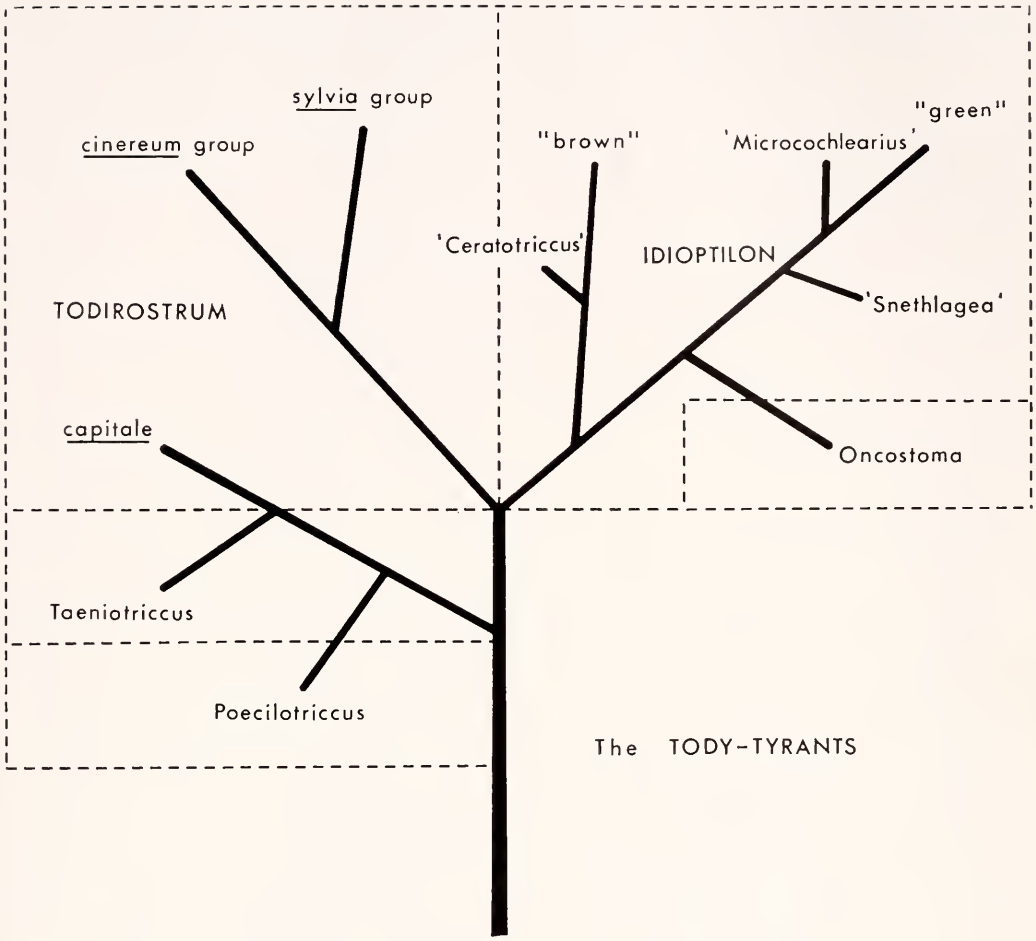

Figure 4. Generic relationships in the Tody-tyrants as commented upon in the text. Dashed lines enclose each lineage whose generic separation warrants continued recognition. Thus "*Ceratotriccus*," "*Microcochlearius*" and "*Snethlagea*" are here grouped into the genus *Idioptilon*. The "brown" species group contains species morphologically intermediate between *Todirostrum* and *Idioptilon*, and is placed within the latter genus on the basis of overall plumage patterns and wing formulae.

incorporated into the basic taxonomy of the group under study. With this in mind, the diagram in Figure 4 includes dotted lines enclosing the generic groups by which, in my view, the Tody-tyrants should now be recognized.

The above suggestions are incorporated into a revision of the broad-billed Euscarthmine tyrannids presented here, along with summaries of the distribution type of each species, as Table 1.

SPECIATION IN *TODIROSTRUM*

Members of the genus *Todirostrum* occur from southern Mexico south throughout tropical and lower subtropical South America to southern Brazil, northern Argentina, and southwestern Bolivia. They are small, secretive birds (16–22 cm, 5–9 gm) generally inhabiting the middle and lower strata of tropical forests and tangled underbrush along forest openings and edges. They forage mostly in thick vege-

TABLE 1. REVISED CLASSIFICATION OF THE TODY-TYRANTS (TYRANNIDAE: SUBFAMILY EUSCARTHMINAE), WITH THE DISTRIBUTION TYPE OF EACH SPECIES INDICATED. SPECIES KNOWN ONLY FROM THEIR TYPE LOCALITY ARE SO MARKED. COLUMNS AND SYMBOLS ARE ADAPTED FROM MAYR AND SHORT (1970) AS FOLLOWS: l = LOCALLY DISTRIBUTED, w = WIDESPREAD; COLUMN A = MONOTYPIC SPECIES, COLUMN B = UNCOMPLICATED POLYTYPIC SPECIES (NUMBER OF DESCRIBED RACES INDICATED IN PARENTHESES), COLUMN C = STRONGLY DIFFERENTIATED POLYTYPIC SPECIES (NUMBER OF POPULATIONS IN PARENTHESES), COLUMN D MARKED WITH X IF SPECIES IS A MEMBER OF A SUPERSPECIES. BRACKETS LINK MEMBERS OF SUPERSPECIES.

Species	A	B	C	D
Poecilotriccus ruficeps		w(4)		
Taeniotriccus andrei	w			
Todirostrum				
capitale			l(2)	
cinereum species group				
calopterum			l(2)	
nigriceps	l			X
chrysocrotaphum		w(5)		X
pictum	w			X
*cinereum**		w(7)		
poliocephalum	l			
maculatum		w(5)		
sylvia species group				
sylvia			w,l(5)	
latirostre		w(6)		X
fumifrons		l(2)		X
plumbeiceps		w(4)		X
russatum	l			X
senex (type)	l			?
Idioptilon				
"brown" species group				
furcatum	l			
rufigulare	l			
mirandae	l			X
kaemferi (type)	l			X
granadense			w(7)	
"green" species group				
nidipendulum		w(2)		
striaticolle		w(5)		
spodiops	l			
zosterops			w(4)	
minor		w(2)		
aenigma (type)	l			
inornatum (type)	l			X
margaritaceiventer			w(7)	X
orbitatum	w			
josephinae	l			
Oncostoma cinerigulare			w(2)	

* Includes *T. viridanum*, recently found sympatric with *cinereum* in nw. Venezuela by Phelps.

tation with periodic, rapid flits, picking arthropod prey from the undersides of overhanging leaves. This characteristic foraging method makes use of their peculiarly long, spatulate bills, the most striking morphologic feature of the genus. Habitat preferences of each species are summarized in Table 2.

Reconstruction of the isolation and differentiation of populations, and their patterns of dispersal leading to today's geographic distributions, are based on four assumptions which must be carefully noted at the outset. The first two are closely related, and critical:

1) The primitive *Todirostrum* ancestor, and all descendent forest inhabiting species, were restricted during continental dry periods to small forest "refugia" within their former ranges. This can be inferred from the observation that, with two exceptions discussed presently, modern distributions in this genus occur exclusively within the forested regions of South America. While many populations are currently widespread, most would have been significantly restricted during any period in which the areas of continental humid vegetation were reduced. Substantial evidence now indicates that vast shrinkage of the continental forests during Plio-Pleistocene times did indeed occur (geological, zoological, botanical, and paleobotanical data summarized by Haffer, 1974). It appears safe to suppose, therefore, that the distributions of forest-inhabiting *Todirostrum* precursors were affected by the fragmentation of their favored habitat.

2) Modern populations with local distributions within the continental forests directly reflect their places of origin and differentiation. A number of these local *Todirostrum* populations currently exist, and all of them coincide with refugium sites proposed by Haffer (1974: 145). Actually, a species originating in one area could have been secondarily restricted to another, wholly different region, thus giving the impression of having differentiated

Table 2. Known or described habitat preferences of species in the genus *Todirostrum*. Reference list for most species is not exhaustive, but selected to include the most important or thorough descriptions available. "Locality data" refers to descriptions of collecting localities or notes on specimen labels.

Species	Habitat	References
chrysocrotaphum superspecies	tropical; forest canopy, forest edges, plantations	Skutch (1972), Terborgh and Weske (1969), Haverschmidt (1968), pers. obs.
calopterum	upper tropical; forest undergrowth near mountains	locality data, pers. obs.
cinereum	tropical, lower subtropical; scrub, open forest undergrowth; coastal mangroves (Cent. Amer.)	Skutch (1930), Slud (1960), Miller (1963), Terborgh and Weske (1969), pers. obs.
poliocephalum	same as *cinereum*	Sick (1968)
maculatum	tropical; forested creek edges, marshy river bottoms; coastal mangroves (Guianas)	Haverschmidt (1955), locality data, pers. obs.
sylvia	tropical, lower subtropical; dense thickets, scrub, forest understory	Miller (1947), Gilliard (1959), Slud (1960, 1964), pers. obs.
latirostre	tropical; dense forest undergrowth, thick tangles, canebrakes along rivers	Olivares (1955), Terborgh and Weske (1969, pers. comm.), locality data
fumifrons	tropical; tangled underbrush, open thickets, savana edge	Haverschmidt (1968), Novaes (1970)
plumbeiceps	subtropical; thick brush, forest edge	Wetmore (1926), locality data
russatum	subtropical; atop cerros in Venezuelan tableland	Mayr and Phelps (1967)
capitale	tropical; forest	locality data

there. Since we have no means of proving otherwise, it is assumed here that any secondary restriction of a species' distribution coincided with the area in which it was initially isolated. Potential historical inaccuracies resulting from this assumption are of little consequence to the present study, since only the most recent geographic relationships among species are of concern here.

3) Splitting populations during periods of forest contraction resulted in extinctions of daughter populations in some refuges. As forest "islands" decreased in size the smaller areas became decreasingly capable of supporting the regional fauna, and extinction rates in each refuge increased (MacArthur and Wilson, 1967). Hence, if a species that was initially split into four or five separate populations survived at all, it may have done so in only one or two of the refugia.

4) Foraging modes and habitat preferences of certain forest populations shifted or generalized to include more open habitats during isolation (because of increased competition within the shrinking forest islands), permitting colonization of open scrub regions during the dry periods. This applies particularly to populations of *T. cinereum* and *T. sylvia,* both of which currently inhabit vegetation types that may

Figure 5a.

Figure 5. Hypothesized patterns of speciation within the *cinereum* (5a) and *sylvia* (5b) species groups in *Todirostrum*. Isolation of ancestral populations (shaded areas) during two dry periods and their directions of dispersal from initial refuge sites are diagrammed. During dry periods populations of *cinereum* and *sylvia* dispersed through regions of open vegetation (solid arrows). Dashed lines outline hypothesized distributions of these species during a recent dry period. The distribution of *cinereum* was restricted during a previous humid period, when the central Amazonian forest had returned. This range contraction (see dashed arrows away from Amazonia in 5a) resulted in the isolation of a population in southeastern Brazil, which became *T. poliocephalum*. During humid periods ancestral populations of the modern forest-inhabiting species dispersed (dashed arrows), but contracted again during a recent dry period (upper right diagrams in 5a and 5b). *Todirostrum maculatum* might not have been fully restricted to a refugium during the recent dry phase given its current preference for mangroves and streamside vegetation, and the ancestral distribution shown here (heavily dotted region in 5a, with question mark) is speculative.

have been widespread on the continent during the dry phases.

With each climatic cycle, a new magnitude of complexity is naturally added to the distribution patterns in any phyletic group. Hence precise ranges of forms existing prior to two or three cycles would be impossible to determine from modern distribution data. For this reason, the following reconstruction begins subsequent to the isolation of three species group precursors from the single *Todirostrum* ancestor.

Figure 5b.

Figure 5 provides a diagrammatic summary of the speciation patterns derived in detail in the following sections.

Cinereum Species Group

Four populations originally isolated from the precursor of this group have apparently survived, currently represented by five species. *T. poliocephalum* probably originated from a southerly advance of the *T. cinereum* progenitor during a subsequent dry period.

T. calopterum currently consists of two divergent races, the nominate (eastern Ecuador and northern Peru) slightly more widespread than *T. c. pulchellum* (southeastern Peru; see Fig. 6). The northern race resembles the other members of this species group, with a green back, black crown, and clear yellow underparts. The Peruvian race, in contrast, has a striking facial pattern with dark malar stripes and deep chestnut loral spots, and its upperparts are entirely black. Assuming that the species originated in one of the two regions to which it is currently restricted (as-

Figure 6. Distribution of three *Todirostrum* species in the *cinereum* species group. The absence of *cinereum* in central Amazonia may be due to the presence there of *T. maculatum* (see text). Diagonal hatching = *cinereum*; dots = *poliocephalum*; squares = two populations of *calopterum* (individual localities).

sumption 2 above), *calopterum* appears to have originated in an eastern Ecuadorian forest refuge (Haffer's large "Napo" refugium). This hypothesis would account for the similarity of the northern race to the other species in the *cinereum* group. The species probably then colonized southward along the post-glacially expanding forests east of the Andes. Its continuous north-south distribution was severed by a return of dry conditions that split the east-Andean forest again into refuges. The southerly population has remained isolated, and its uniquely divergent plumage attests to a long separation from the northern race.

Distribution and current geographic variation in the *chrysocrotaphum* superspecies are illustrated in Figure 7. The clear yellow underparts of the species group precursor have been retained in *nigriceps* and three races south of the Amazon River. Particularly below its confluence with the Rio Negro, the Amazon is a complete geographic barrier separating streaked from unstreaked populations. Geographic isolation even between the two forms on either

Figure 7. Distribution of the *Todirostrum chrysocrotaphum* superspecies. Representations of the main morphologic types are shown in their approximate geographic positions. From left to right, the five described races of *chrysocrotaphum* are: *guttatum*, *chrysocrotaphum*, *neglectum*, *similis*, and *illigeri*. See text for detailed analysis of this variation.

side of the Rio Negro has been borne out by collections along the lower part of the river. The superspecies thus presents a reliable record of the different forest regions within which its initial populations differentiated.

As previously surmised, the breast streaks of *pictum* and *guttatum* evolved secondarily on the previously clear-breasted form. The original *chrysocrotaphum* stock was therefore isolated either in the southeastern Peruvian forests or in one of the northwestern Colombian forest refuges since these two areas retain clear-breasted populations. During a period of forest expansion the population then spread through the western Amazonian region (where streaks later evolved) to the other region of currently clear-breasted birds. A Peruvian precursor (of *chrysocrotaphum*) would presumably have had sufficient time before colonizing across the Andes to evolve certain of the patterns it carries today. *T. nigriceps*, however, lacks any trace of the distinct eye stripe of *neglectum*. Furthermore, *nigriceps* retains the white throat characteristic of most other *Todirostrum* species but lost in *neglectum*. Thus it appears that the superspecies precursor differentiated in one of the refuges of northern Colombia (see Fig. 5a), probably during the same period in which the initial *calopterum* population was isolated in the Napo refuge.

Following initial isolation of the species, the clear-breasted population crossed the

Andes and probably spread through much of its present Amazonian range. The subsequent pattern of differentiation, caused by the return of dry conditions, can be surmised from Figure 7. A distinctive population called *pictum* now ranges from the Guianas west to the Rio Negro. *T. c. neglectum,* with its unstreaked breast, yellow eye stripe, and solid black forecrown, occurs from eastern Bolivia north to the Amazon. The remaining races variously combine characters from both forms. The necklace and loral spot of *pictum* have spread westward, while the eye stripe of *neglectum* has spread north and east. This distribution of characters indicates that forest refuges in the Guianas and in southern Peru were the major centers for Amazonian differentiation during the last major dry period.

As the forest returned, the southern population spread eastward to the Atlantic coast, where it is represented today by the race *illigeri.* The characters of *pictum* have crossed the upper Amazon in western Brazil and Peru, hence certain specimens still assignable to *neglectum* show traces of the necklace and loral spots. Loral spots have now spread eastward again along the southern bank of the Amazon, currently terminating in the race called *similis* west of Rio Tapajoz. *T. c. guttatum,* in eastern Ecuador and northwestern Brazil, shows the full array of characters from both original populations (see Fig. 7). All racial characters in *chrysocrotaphum* shown in the figure are clinal.

The current distribution of characters near the mouth of the Rio Negro and north into southern Venezuela remains somewhat puzzling. The breast and loral markings of *pictum* have moved westward, while the conspicuous eye stripe of *neglectum* remains restricted to the west bank of the Rio Negro and Rio Branco. This is probably due to the sequence by which *pictum* expanded westward, and may indicate a double invasion of the region from the Guianas. The first invasion contributed breast streaks and loral spots to the west, before open vegetation in middle Amazonia (Haffer, 1967) again separated the eastern and western populations. Upon subsequent dispersal of both populations back toward the Rio Negro, *guttatum* and *pictum* then excluded each other on their respective banks. While a complete series of specimens from northern Brazil may still prove that the forms interbreed there, the available evidence indicates that isolation is complete. *T. pictum* thus represents as clear a geographic representative as *nigriceps* and *chrysocrotaphum* within this interesting superspecies.

Todirostrum cinereum, the most widespread species in the genus, apparently developed its more open habitat preferences during its initial isolation from the species group precursor. The closely related southeast Brazilian endemic, *T. poliocephalum,* occupies similar vegetation types, commonly including garden bushes and shrubbery (Sick, 1968). This latter form differs from *cinereum* only in its more conspicuous yellow lores and distinctly greener back and tail. Their distributions overlap only marginally in southeastern Brazil (see Figure 6) and the southeasterly occurrence of *cinereum* appears to be a reinvasion from the northwest after the population that became *poliocephalum* had been isolated.

The hypothesis that *cinereum* originated in the north (Fig. 5) is supported by two additional lines of evidence. First, the two branches of its range, the races *coloreum* in the south and *cearae* to the north, differ rather sharply in color and measurements, while populations to the west of each differentiate along clines. The indication is that the north and south Brazilian forms colonized independently from a common population northwest of both, and have not shared recent contact with each other. Second, *cinereum* is extremely common in a variety of habitats in northern South America, and occurs in tropical regions throughout Central America as far north as

Figure 8. Distribution of *Todirostrum maculatum*. Compare its extensive Amazonian distribution with that of *T. cinereum* (Fig. 6), a possible ecological competitor which appears to be excluded from central Amazonia. Diagonal hatching = overall geographic range of *maculatum*. Dots indicate known collecting sites for the species, including one questionable locality.

Vera Cruz, Mexico (Griscom *et al.*, 1957). While fairly common in certain regions of Brazil, it is not nearly as widespread there as might be expected had it originated in the south. The species appears to be better adapted to the more northerly scrub regions, having secondarily advanced south and east into Brazil.

The most recent reappearance of the Amazonian forest probably broke a nearly continuous distribution of *cinereum* in western Amazonia, where it now occurs only along the base of the Andes.

It currently appears that the occurrence of *Todirostrum maculatum* along river margins in Amazonia contributes to the absence of *cinereum* throughout much of that region (compare Figures 6 and 8). Comparative ecologies of these species are presently being studied to test this hypothesis, but preliminary field data from Peru and comments by Haverschmidt (1968) already support it. In southeastern Peru (dept. Madre de Dios) *maculatum* inhabits thickly vegetated, early successional margins along rivers, especially bordering beaches, where it forages one to ten meters from the ground (Fitzpatrick, unpublished data). In many respects these habits strongly resemble those of *cinereum* in the Apurimac Valley in central Peru (dept. Ayacucho), where *maculatum* does not occur (Terborgh, personal communication). Furthermore, while *cinereum* is a common mangrove inhabitant in Central and northwestern South America, it is apparently restricted to the drier habitats in Surinam, where *maculatum* has replaced it as the common mangrove Tody-tyrant (Haverschmidt, 1968).

While collecting in the cerrado region of central Brazil has been spotty, that area

does contain a certain fraction of endemic, locally adapted species, including another small Euscarthmine flycatcher (*Euscarthmus rufomarginatus*; Sick, 1965, 1966). It may be that the absence of *cinereum* in central Brazil is also due to the presence there of a better adapted complex of competing species.

The origin and differentiation of *T. maculatum* can be inferred by examining its present clinal variation along the Amazon (distribution shown in Fig. 8). This consists of a gradually lightening crown from the black-crowned race, *amacurense*, in the Orinoco delta (Eisenmann and Phelps, 1971) to the light grey or green crowns in *signatum* of eastern Peru (Zimmer, 1940: 5–7). There appears also to be a concomitant broadening of the breast streaks toward the west. Both clines leave the Guyana birds much closer to the presumed plumage of the species group percursor (as hypothesized in the taxonomic comments), indicating that *maculatum* originated in a northeastern coastal refuge. Lightening of the crown would have occurred subsequently, as the species spread westward throughout Amazonia. The species is now abundant in mangroves along the Atlantic coast of the Guianas and Venezuela, and occurs along the margins of streams and rivers in the Amazon basin.

Preference for the river margin habitat perhaps explains why, in contrast to the canopy-dwelling *chrysocrotaphum* representatives, *maculatum* does not occur in distinctly isolated geographic forms. During periods of complete separation between true forest populations, such as those in the *chrysocrotaphum* superspecies, the distribution of *maculatum* was probably more continuous along locally moist stream edges, thickets, and canebrakes. Thus *maculatum* populations might have undergone only limited periods of isolation during Pleistocene dry phases, if in fact the species was fragmented at all during that time.

Sylvia Species Group

The distribution of *sylvia* coincides with the scrublands of southern Central America and northern South America (Fig. 9). This species apparently shifted its ecological preferences in a fashion similar to *T. cinereum,* during or immediately following its original isolation. In a subsequent dry period it then spread north into Central America and south along the Atlantic coast. This expanded distribution was interrupted by the return of the modern forests, which restricted nonforest inhabitants as elaborated by Haffer (1967). Two uncommon, relict populations mark the once larger range of *sylvia*: one inhabits the dry, inland savanna region of the Guianas (*T. s. sylvia*) and the other, the caatinga scrub of northeastern Brazil (*T. sylvia schulzi*).

The ecological position of *sylvia* relative to other small Tyrannid species is of considerable interest, though its significance to the species' patterns of distribution and abundance has yet to be worked out. Slud (1964) indicates that *sylvia* generalizes its habitat requirements to include more open shrubbery and second growth forests in regions where *T. cinereum* or *Oncostoma cinerigulare* (a Euscarthmine species closely related to *Todirostrum*) or both are locally absent. This observation, which warrants further field investigation, suggests that *sylvia* is competitively inferior in habitats shared with these relatives. This may explain the rarity or absence of *sylvia* in otherwise suitable habitats throughout northern South America, where *cinereum* is common and widespread. The disappearance of *sylvia* in these areas, initiated by the reduction of its habitat into local islands, may thus have been catalyzed by the presence of a highly successful, congeneric competitor.

T. latirostre is the only wide ranging species in the "*latirostre* complex" and its pattern of variation gives strong evidence for the sequence by which the complex diverged. In eastern Ecuador and north-

Figure 9. Distribution of the six species comprising the *Todirostrum sylvia* species group. All five members of the "*latirostre* complex" (which excludes *sylvia*) remain allopatric, though *T. senex* is known only from its type locality on the Rio Madeira (Borba). Diagonal hatching downward to left = *plumbeiceps* superspecies (triangles = collecting localities for *russatum*); stippling = *latirostre* superspecies (open circles = collecting localities for *fumifrons*); diagonal hatching downward to right = *sylvia* (X = collecting localities for the two eastern races, *sylvia* and *schulzi*).

eastern Peru, its dark grey crown, cinnamon-buff auricular and ocular regions, light buffy throat, and tawny wingbars all strongly resemble the plumage of *T. plumbeiceps*. Fading of each of these characters south and east of Ecuador results in southeasternmost specimens that closely approach the plumage of *T. fumifrons*. The latter is a rare species inhabiting scrub and forest-edge habitats east of the range of *latirostre*. The most informative feature of the plumage pattern of *latirostre* is its remarkable resemblance, in the region of the former Napo refuge in eastern Ecuador, to that of the *plumbeiceps* superspecies. This is evidence that the Ecuadorian population of *latirostre* most closely represents the primitive one, and that the species origi-

nated there. This hypothesis is strengthened by the generally northeastern Amazonian distribution of the species today.

Two alternative patterns of speciation in this species group can be hypothesized. First, a recent dry period could have isolated each separate population from a single, wide-ranging species. *T. latirostre* would then have spread eastward into its current range following the return of forests there. This hypothesis, however, fails to account for the particular similarity between *plumbeiceps* and *russatum*, which appear to be immediately descendant from a form already distinct from the *latirostre-fumifrons* ancestor. Furthermore, *plumbeiceps* is currently represented by a Bolivian population which itself has differentiated into recognizable races (Zimmer, 1940). This Bolivian isolation must have occurred during a major dry period which had already isolated *russatum* in Venezuela, since Bolivian specimens of *plumbeiceps* are much closer to those from southeastern Brazil than to the isolated *russatum*.

It appears, instead, that a parent stock for this species group was initially split into a population north of the Andes, which became *sylvia*, and one to the southeast which gave rise to the *latirostre* complex. As open vegetation continued to spread, the cis-Andean form was reduced to isolated populations in the eastern Ecuadorian forests and in southeastern Brazil (see Fig. 5b). This hypothesized sequence is consistent with the observed similarity between *plumbeiceps* and the population of *latirostre* occupying the region of the Napo refuge. As forests returned, the Napo species spread eastward and the Brazilian form spread north and west. As a subsequent dry period began (probably the last major continental arid phase), the southern species had left an isolate on the Venezuelan highlands (now *russatum*) and possibly one in central Brazil (*senex*) before being reduced to its Bolivian-Brazilian range. Further habitat reduction then caused the current gap in the range of *plumbeiceps* itself (see Fig. 9). The other cis-Andean species, again reduced to its refuge in eastern Ecuador, left an isolate in northeastern Brazil which differentiated into the two races of *T. fumifrons*. Today, *latirostre* has followed the forest and river valleys back eastward into central and southern Amazonia following its last isolation. Its plumage in the drier forested valleys of the Brazilian cerrado appears to be responding to pressures similar to those which affected *fumifrons*. In these areas it has become dull and faded and thus strongly resembles the pattern of its sister species.

The present distribution of *latirostre* reaches, but does not overlap, those of *plumbeiceps* to the south and *fumifrons* to the east. It appears to represent a situation in which close congeners, adapted to their respective place of origin, exclude each other across an intermediate area. Confirmation of this hypothesis requires precise ecological information from different areas within the ranges of each respective species, and at their junctions. These measurements, for most or all species in the group, will be crucial to the completion of the biogeographic analysis initiated here.

Capitale Species Group

Todirostrum capitale clearly originated in the forests of the Napo refuge, to which area it remains almost exclusively restricted (Fig. 10), and appears to represent a deep forest relict of a third population isolated from an original *Todirostrum* ancestor. From the Napo region, its distribution has probably undergone expansions and contractions, but only two specimens have been collected that attest to the species' occurrence elsewhere. The southerly population, *T. capitale tricolor*, originated in a south Peruvian refuge following a southward colonization by the Napo population. It has now extended along the lowland forests of the Rio Madeira drainage into western Brazil, where it apparently remains rare.

Several divergent characteristics of the

Figure 10. Distributions of *Todirostrum capitale*, *Taeniotriccus andrei*, and *Poecilotriccus ruficeps*. The latter two genera are monotypic. Morphologic and biogeographic evidence (see text and Figure 3) indicate that these three species comprise a single, relict Tody-tyrant lineage. Vertical hatching = distribution of *Poecilotriccus ruficeps* (small dots = collecting localities); horizontal hatching = distribution of two populations of *Todirostrum capitale* (triangles = collecting localities); stippling = distribution of *Taeniotriccus andrei* (open circles = collecting localities).

species, discussed in the taxonomic comments above, suggest that the *capitale* lineage is at least as old as the two major *Todirostrum* species groups. Most important, the pronounced sexual dimorphism in *capitale* implies a long period of behavioral as well as morphologic divergence, and attests to the species' long isolation from the other *Todirostrum* species. In fact, the *capitale* lineage is probably much older than the two larger species groups, and appears to contain two additional, equally divergent relicts, as shown in the taxonomic section. In addition to their peculiar plumage patterns and bill structures, each of the three species exhibits a secondarily restricted distribution, further indicating the age and relict position of this lineage relative to the other two species groups.

Although *Poecilotriccus ruficeps* is locally common within its range, its distribution is restricted to a narrow forest zone between 1900 and 2700 m in the Andes from northern Peru to extreme western Venezuela (Fig. 10). Without adequate field data it is impossible to speculate on the precise ecological pressures constraining the distribution of *ruficeps*. However, nearly every Euscarthmine species occupies lowland habitats, and *ruficeps* undoubtedly differentiated originally as a tropical forest species. Narrow altitudinal distributions like that of *ruficeps* may result from invasions into a forest species' original range by one or more species with superior competitive potential. Individuals of the original species that are able to survive and reproduce at higher altitudes eventually provide refuge for the species, gradually forced from its original lowland habitat

through competition. All such shifts are limited by analogous competitive pressures from species already occurring higher on the slopes. Data provided by Terborgh (1971), Terborgh and Weske (1975), and Diamond (1972) give compelling evidence for the action of competition along altitudinal gradients on the distributions of montane birds.

Presumably following range expansions and contractions by *capitale* and *andrei*, both of these species appear to have become rather rare and local. This, too, probably resulted from radiation within closely related Tyrannid species placing increasing competitive pressures on the earlier evolutionary line. As additional successful species were periodically added to the forest fauna, certain species necessarily decreased in abundance. Their overall distributions may thus have been reduced to regions of particularly favorable habitat (possibly the case with *andrei*) or restricted to ever-diminishing zones in which some minimum population level could be maintained (as in *capitale*). These two species thus appear to be engaged in—and possibly losing—an "evolutionary race" as their related competitors continue to radiate. As their populations decline, they either diverge sufficiently in a direction that reduces this competition (causing the peculiarly divergent structures, plumages, and presumably behavior of both *capitale* and *andrei*), or they are ultimately driven to extinction by their competitive environment. A slightly more detailed description of this process is presented in the discussion section.

IDIOPTILON AND RELATED SPECIES

As previously discussed, species in *Idioptilon* fall into two plumage types, the "brown" and "green" assemblages, which correspond phyletically with the species groups in *Todirostrum*. The "brown" lineage appears to be phylogenetically intermediate between *Todirostrum* and the typical ("green") *Idioptilon* lineage. The interesting and revealing distribution patterns in the relict "brown" species group (Fig. 11) will be discussed briefly here.

Idioptilon rufigulare is a perfect example of an excessively rare montane relict species. It is known from six specimens, all of which were collected between 1200 and 1500 m on isolated Andean ridges in Peru and extreme northern Bolivia. This restricted altitudinal distribution was recently confirmed by J. Terborgh (personal communication) in central Peru, where the species was uncommon but present at 1500 m on a small ridge separated from the main Andes by 100 km of lowland forest. Perhaps once a wide-ranging species, *rufigulare* is now restricted to a narrow, middle altitude zone on certain slopes which, by virtue of their reduced avifauna, are relatively free of lower and higher altitude competitors (Terborgh and Weske, 1975).

Few ecological data are available for the *I. mirandae* superspecies. Clearly, however, the limited ranges of the two members, separated by more than 2000 km, reflect a tiny fraction of their common ancestral distribution in eastern Brazil. Similarly, *furcatum* (formerly "*Ceratotriccus*" *furcatus*) currently occupies an extremely restricted range within the wooded coastal hills of Rio de Janeiro, Brazil.

Of the "brown" *Idioptilon* species, only *granadense* does not appear to have become significantly restricted in its distribution. Morphologically, however, this species is the most divergent in its genus, and, more significant, it is one of only three in the genus that occur at higher elevations. (The other two, *rufigulare* and *spodiops*, are rare mountain relicts.) In isolated north Andean ranges, *granadense* occurs in an altitudinal zone about 1000 m wide (1500 to 2400 m in the Sierra Nevada de Santa Marta, Colombia; 1800 to 2900 m in the Sierra de Perija, Venezuela). On the main Andean slopes, in a more crowded competitive community, its altitudinal limits are more restricted (2280 to 2600 m, west of the Apurimac River, central Peru; Terborgh

Figure 11. Distributions of the five populations in the "brown" *Idioptilon* species group, showing known collecting localities for each species. All but *granadense* are extremely rare, relict species. The upper subtropical altitudinal range of *granadense* (2200–2600 m in central Peru) differs from all other *Idioptilon* species, and appears to be a response to the radiation of assemblages of lowland competitors which has driven the remaining members of this species group close to extinction. Small dots = *granadense*; large dots = *rufigulare*; squares = *mirandae* superspecies (closed = *mirandae*, open = *kaemferi*); triangles = "*Ceratotriccus*" (*Idioptilon*) *furcatus*.

and Weske, 1975). It remains an upper cloud forest inhabitant throughout its range, however, and this habitat is shared by no other close relative.

Distribution and morphologic divergence in the brown *Idioptilon* species group appear analogous to those characterizing the *capitale* lineage in *Todirostrum*. Members of both groups show relict distributions or divergent characters, or both, compared with the other members of their respective genera. As in the *capitale* group, the five brown *Idioptilon* species apparently comprise an early phylogenetic divergence from the ancestral lineage. Four members have been fragmented or compressed into restricted distributions within the forested tropics and subtropics. The fifth was secondarily forced up into an altitudinal zone that remains unique to the genus. As discussed in the next section, the pressures forcing these early species into their relict conditions apparently resulted from the continued production of new, competitively superior relatives within the tropical forests.

The remaining members of the genus *Idioptilon*, together with the monotypic

genera *Microcochlearius*, *Snethlagea*, and *Oncostoma*, constitute the "green" assemblage. These eleven species appear to form another monophyletic subgroup within the broad-billed Euscarthmine Tyrannids. Additional data on behavior and ecological relationships are required before affinities and distributional patterns in this difficult group can be satisfactorily commented upon. Research is currently underway which may provide some of this information.

DISCUSSION

The *Todirostrum capitale* lineage and the "brown" *Idioptilon* species group are extreme cases illustrating the final stages of a speciation-dispersal-extinction process that appears to be a continental analogue of the "taxon cycle" characterizing island faunas (Wilson, 1961; Ricklefs and Cox, 1972). In this section, some illustrative examples of the main stages in the process precede a brief discussion of the dynamics of this important phenomenon.

In the following outline, nine types of distributional relationships are delimited which summarize the biogeographic "life history" of certain lowland South American bird species. By no means are these categories meant to include all probable intermediate stages in the process to be discussed; rather, only those stages are chosen which characterize members of the Tody-tyrant group dealt with in this paper, and the examples are included under each category.

1) Newly isolated populations, presumably still representing a single species.
   a. races of *Todirostrum sylvia*
   b. races of *Idioptilon margaritaceiventer* ("green" assemblage)
2) Populations apparently isolated prior to the last major dry period; significantly diverged but not yet in secondary contact.
   a. *Todirostrum nigriceps* — *T. chrysocrotaphum*
   b. *Todirostrum latirostre* — *T. fumifrons*
   c. *Todirostrum plumbeiceps* — *T. russatum*
3) Closely related populations currently in contact but not overlapping (parapatric).
   a. *Todirostrum chrysocrotaphum* — *T. pictum*
   b. *Todirostrum latirostre* — *T. plumbeiceps*
4) Well-differentiated species, partly sympatric but apparently excluding each other geographically over a broad contact zone; presumably similar ecologically.
   a. *Todirostrum maculatum* — *T. cinereum*
   b. *Todirostrum cinereum* — *T. poliocephalum*
   c. *Todirostrum cinereum* — *T. sylvia* (entirely sympatric, but *sylvia*'s range much contracted in presence of *cinereum*; see discussion in speciation section)
5) Well-differentiated species, mostly or entirely sympatric; many examples, especially *between* species groups.
   a. *Todirostrum maculatum* — *T. chrysocrotaphum* superspecies
   b. *Todirostrum maculatum* — *T. latirostre*
   c. *Todirostrum plumbeiceps* — *T. poliocephalum*
6) Species presumably widespread at one time, now reduced to one or more localized ranges; populations probably declining; often morphologically divergent.
   a. *Todirostrum capitale*
   b. *Todirostrum calopterum*
   c. *Idioptilon furcatum* (formerly *Ceratotriccus*)
   d. *Idioptilon mirandae* superspecies
7) Lowland species still rather widespread, but very rare; either reduced to low absolute density or restricted to rare habitats.

a. *Taeniotriccus andrei*
b. *Microcochlearius josephinae*

8) Species with wide altitudinal tolerance, currently forced up to higher altitudes by lowland competitors.
Example: probably *Todirostrum calopterum pulchellum,* though conclusive data are lacking; northern race still occurs in lowland forests, but *pulchellum* is rare and restricted to upper tropical zone in southeastern Peru.

9) Species related to lowland forms but now restricted to narrow, higher altitudinal zone in the Andes.
a. *Idioptilon rufigulare* (1200–1500 m)
b. *Poecilotriccus ruficeps* (1900–2700 m)
c. *Idioptilon granadense* (1800–2900 m, Venezuela; 2200–2600 m, Peru)

Plio-Pleistocene radiation of the suboscines apparently occured with relatively little competition from other avian groups in South America. Five major suboscine families comprise well over half of the continent's passerine fauna, and the 302 Tyrannid flycatchers, representing one tenth of South America's 2900 land bird species (Smith and Vuilleumier, 1971), radiated into an almost unparallelled array of morphologic groups (summarized by Keast, 1972).

Haffer's extensive work on the zoogeography of lowland South America has given us a clearer picture of how such radiation came about, emphasizing that speciation has been a repetitive process for millions of years. During continental dry periods, presumably associated with world-wide glacial episodes, forest species were split into isolated populations each with the potential for differentiating into a new species. During humid climatic phases, species inhabiting open, nonforest vegetation underwent similar fragmentation. Faunal dispersal within expanding vegetation zones resulted in the splitting of newer species into additional arrays of potentially differentiating populations during a subsequent climatic cycle.

A geometric increase in species numbers theoretically associated with periodic fragmentations of dispersing populations is naturally damped by ecological factors. Members of each phylogenetic lineage face increasing competitive pressure as the number of closely related species on the continent increases. The probability that regions potentially available for dispersal might already be occupied by related forms increases with the rising number of species in each taxon. In each such lineage, therefore, dispersal of new forms grows increasingly restricted.

Survival of each population hinges upon one of two requisites: 1) it must occupy, either initially or secondarily, an ecological position sufficiently different from those occupied by sympatric species; or, 2) it must maintain a competitive superiority sufficient to cause the decline and eventual extinction of ecologically similar species (e.g., MacArthur, 1972). Radiation within a taxon, and over regional habitats in general, is thus mediated by continual extinctions of new as well as established populations. Extinctions in this context result from competitive interactions in two situations: 1) the regional dispersal of species into areas occupied by competitively inferior species, and 2) island effects within the shrunken areas of the forest refuges (MacArthur and Wilson, 1967).

The dynamic interplay between speciation and extinction has, in short, caused net species compositions within most taxa and over entire geographic areas to move toward equilibrium levels. This process is diagrammatically illustrated in Figure 12.

A number of phenomena variously associated with the process described here are reflected in the current distributions of bird species in lowland South America. Four points will be briefly discussed that appear to be critical to our interpretation of the nine categories of tyrannid distributions presented at the beginning of this section.

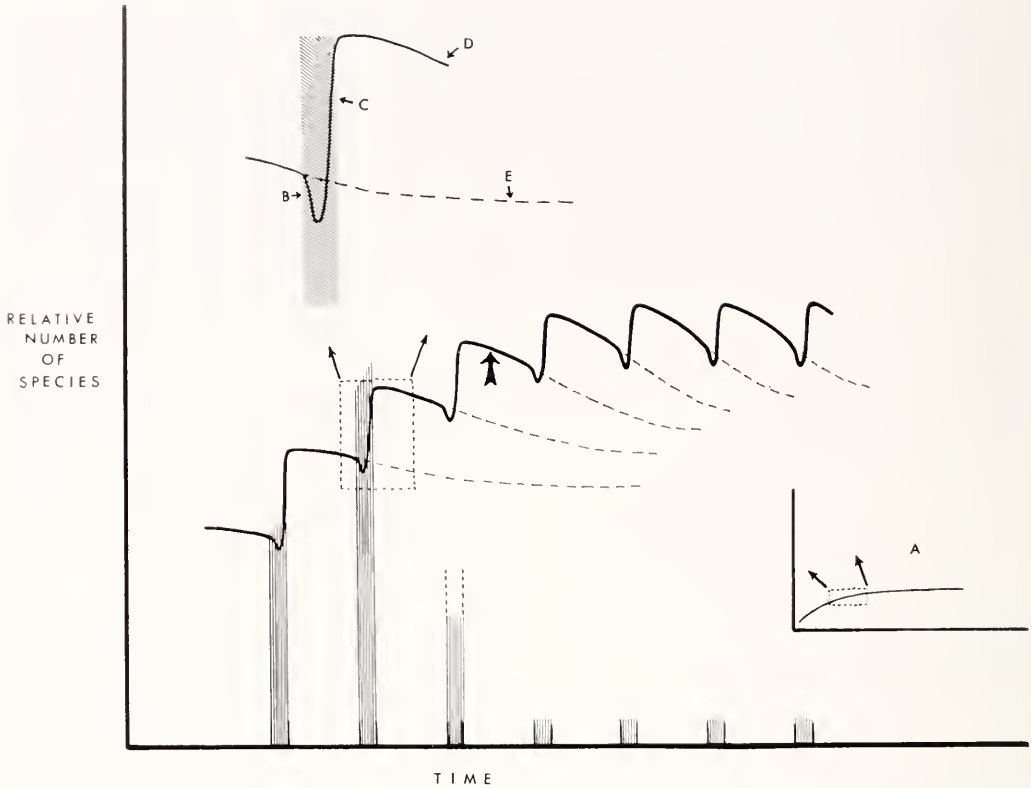

Figure 12. Schematic changes in the relative number of species in the Amazonian forest over time. Shaded areas represent periods of forest fragmentation, associated with dry climatic periods, which split forest species into numerous potentially differentiating populations. New species disperse as the forest returns. These periodic increases in species number are gradually offset by extinctions as competition increases, causing the overall Amazonian diversity to level off at some potential equilibrium value (A). One cycle is shown in detail in the upper left: as the forest contracts, island effects reduce slightly the total number of species (B); differentiation of remaining populations causes an increase in the number of reproductively isolated forms (C); as these disperse with the returning forest, competitive interaction forces species toward extinction, gradually reducing the total number of species (D), which would theoretically smooth out to some stable species composition (E) if the forest remained intact for a long enough period. Note that this stable value increases by smaller increments with each cycle. Heavy arrow indicates hypothesized present position along the species abundance curve.

1) As the number of species increases within a large region like the Amazonian forest the number of forms with small, localized ranges correspondingly increases. Examples of these were used by Haffer (1969) in his reconstruction of forest refuge locations, but few discussions of the ecological implications of such endemics have appeared to date. Endemic species within the Amazonian forest result from the mutually depressing effects on dispersal potential exerted on each other by related species as each spreads from its respective place of origin. In certain groups of species, each maintains sufficient competitive advantage in its original geographic location to exclude the others from its range. This results in the mosaics of parapatric species illustrated abundantly by Haffer (1974), and by the Tody-tyrants in categories 3 and 4 in the examples presented above.

In other cases, the competitive superiority of a dispersing species over certain others may gradually restrict the distribution of

the latter as the superior species grows increasingly widespread. Ultimately the inferior species will vanish completely, but not before a period of gradually diminishing success within its limited range. Because of the variable and potentially great length of this period, we expect to find at any point in time species representing various stages of this contraction (category 6 above). Alternatively, the same gradual decrease in a species' abundance could occur without a corresponding decrease in its geographic distribution. This type of decline might characterize species occupying peculiar, locally distributed habitats, each patch of which would require separate colonization by the complex of superior competitors. A species' overall population could thus decline toward extinction while still occupying a wide range (category 7).

2) An invaded, declining species can alter its mode of habitat utilization and thus escape the competitive pressure causing its decline. In its extreme, this evolutionary strategy might result in a total habitat shift. These types of ecological shifts are discussed by Hamilton (1962) and MacArthur *et al.* (1966) among others. As discussed in the varied literature regarding "character displacement" (reviewed by Grant, 1972), changes in morphology or behavior or both are normally associated with such ecological shifts (as in category 6, above).

3) A shift in altitudinal tolerance can afford refuge for certain populations otherwise doomed to extinction. This process is discussed with respect to Diamond's data on New Guinea bird distributions by MacArthur (1972: 73). As an invading lowland species becomes increasingly common, successful populations of the diminishing species situated up a mountain slope might begin adapting to microclimatic differences associated with the slightly higher altitude. If the species grows sufficiently more successful at the higher altitudes than its lowland competitor, each will have assumed a geographic refuge within which it cannot be forced toward extinction by the other. Given their inability to stably coexist within a habitat, the pair would thus exclude each other altitudinally (categories 8 and 9). This process might happen repeatedly along mountain ranges, resulting in the "stacking" of species along altitudinal gradients documented by Terborgh (1971) and Diamond (1972).

4) All changes by which a species shifts away from competitors occur most readily in species with small ranges, where gene flow is sufficiently localized to allow rapid spread of more competitively successful morphological or behavioral adaptations. It therefore becomes increasingly easy for a declining species to diverge into a new ecological role as its range is reduced, resulting in the "evolutionary race" introduced earlier with reference to the relict and divergent *T. capitale* lineage. As a species grows decreasingly capable of competing successfully within the community its range or abundance or both diminish. In species with very small ranges (category 6), genetic pressures normally inhibiting rapid changes might be sufficiently low to permit the spread of adaptations enabling the declining species to coexist with its former competitors. Species that are unable to change fast enough or far enough eventually "lose the race" and decline to extinction.

Because of the recency of the last major climatic shift, numbers and distributions of South American bird species are far from stable at this time (Fig. 12). Certain local regions of open vegetation in Venezuela, for example, presently much reduced from their former area, apparently remain richer in species diversity than might be expected on the basis of their small area. Competition and extinction rates presumably remain high in these areas. Forest regions that remained intact during Pleistocene dry periods appear to be zones in which endemic species, which have survived but are declining, now co-occur with a dispersing, pan-Amazonian fauna. The result is an unstably large number of species

in these zones compared with the avifauna in the surrounding forest. Terborgh (1973) discusses the kinetics of these historical components to local and continental species diversity with respect to plant communities.

Evidence from the Tody-tyrant distributions presented here supports the assertion that avian distributions within Amazonia are not currently in a steady state. Certain populations are probably still dispersing, other local endemics appear doomed to extinction. However, huge time periods are undoubtedly required for dispersing species to force others entirely out of existence. Indeed, the continent is not likely to remain in its present condition long enough for its fauna ever to settle into a stable composition. Rather, a new cycle of isolations and dispersal will again scramble the distributions of its species, and the dynamic processes outlined above will begin on a new array of populations. These geographic processes appear to have been the prime generators of the diverse avian composition inhabiting the South American lowlands.

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Chelodina parkeri, A New Species of Chelid Turtle from New Guinea, with a Discussion of *Chelodina siebenrocki* Werner, 1901

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CHELODINA PARKERI, A NEW SPECIES OF CHELID TURTLE FROM NEW GUINEA, WITH A DISCUSSION OF *CHELODINA SIEBENROCKI* WERNER, 1901

ANDERS G. J. RHODIN[1] AND RUSSELL A. MITTERMEIER[2]

ABSTRACT. *Chelodina parkeri*, a new species of chelid turtle from New Guinea, is described. Seventeen specimens of the new species are compared to a series of 27 specimens referable to *Chelodina siebenrocki* Werner, 1901, also from New Guinea. *C. parkeri* differs from all other *Chelodina* species in having a light, vermiculate color pattern on the dorsal surface of the head and the mandible. Various other shell and skull characters also differentiate it from other *Chelodina*. *C. parkeri* is endemic to southern New Guinea and is apparently restricted to large inland grass swamps surrounding Lakes Murray and Balimo and the Fly and Aramia Rivers. It is most closely related to *C. siebenrocki*. *C. siebenrocki* is found on the south coast of New Guinea and on certain islands in the Torres Strait. It is most closely related to *Chelodina rugosa* Ogilby, 1890 from northern Australia and may be synonymous with this species. However, the small amount of northern Australian material currently available makes it impossible to draw a conclusion concerning the relationship of these two animals.

INTRODUCTION

The chelid turtle genus *Chelodina* is restricted to Australia and New Guinea and is composed of seven living species divided into three species groups (Burbidge, 1967; Burbidge, et al., 1974; Goode, 1967). The status of two members of species group B—*Chelodina rugosa* Ogilby, 1890, from northeastern Australia (type locality: Cape York, Queensland) and *Chelodina siebenrocki* Werner, 1901 (type locality: German New Guinea)—has not been clear. The major problem has been the lack of a sufficiently large series for taxonomic studies. The only descriptions available of *C. rugosa* and *C. siebenrocki* are the original ones. These are based exclusively on external characters and are inadequate for comparative purposes. No osteological descriptions have been made, locality data from museum specimens have never been carefully checked and nothing has been published on the habitat of either species.

Over the past few years, Fred Parker of New Guinea has provided the Museum of Comparative Zoology at Harvard University (MCZ) with an excellent series of New Guinean chelid turtles, the largest ever collected. Twenty-one specimens in this series are referable to *C. siebenrocki*[3]. While studying the Parker series with the hope of clarifying the *C. siebenrocki-C. rugosa* problem, we found eight specimens of a previously undescribed *Chelodina* species.

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[3] The type specimen of *C. siebenrocki* was lost during World War II (G. Peters, personal communication). However, Werner's (1901) description of this turtle includes photographs of the carapace and plastron of the type (Fig. 1). On the basis of the very close resemblances of Parker's 21 specimens to the type photographs and original description of *C. siebenrocki*, we have concluded that Parker's animals represent *C. siebenrocki*.

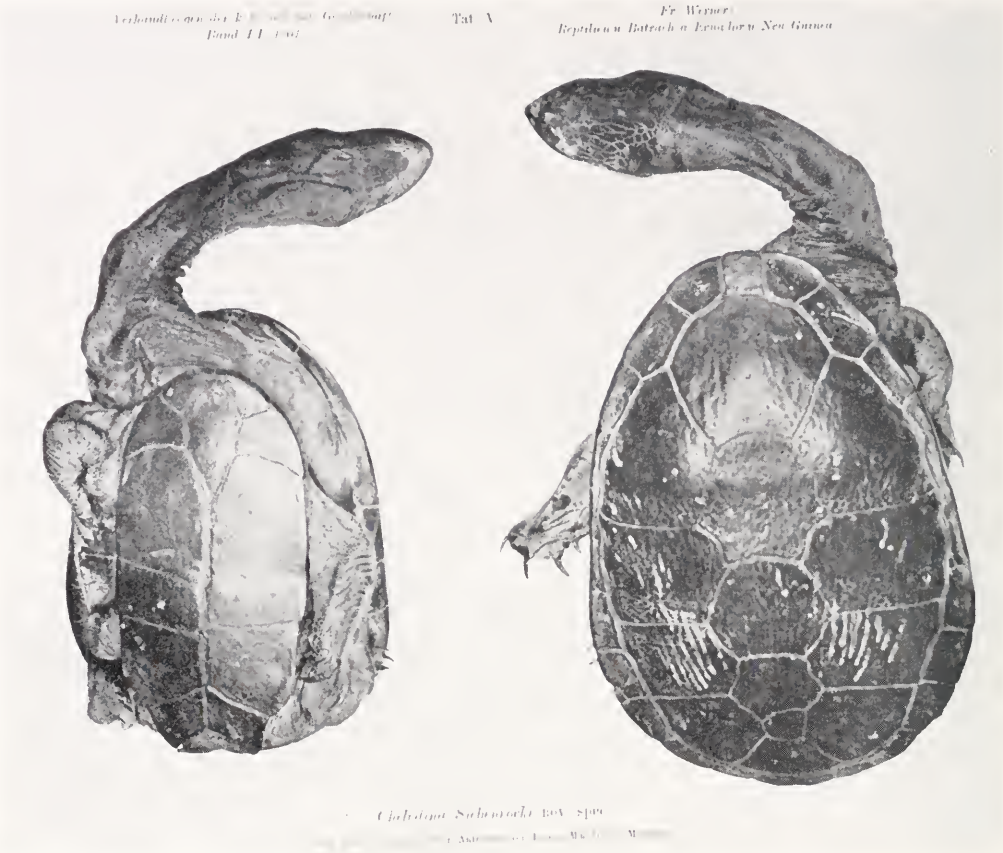

Figure 1. Ventral and dorsal views of the type specimen of *Chelodina siebenrocki* from Werner (1901).

In addition to the 21 Museum of Comparative Zoology specimens, we have examined six other turtles referable to *C. siebenrocki*. These include four collected by Parker and deposited in the Australian Museum in Sydney (AMS) and the American Museum of Natural History in New York (AMNH), and two collected by Müller in 1886 and deposited in the Staatliches Museum für Naturkunde in Stuttgart (SMNS)—bringing the total to 27. In addition to the eight specimens of the new species collected by Parker for the MCZ, we have examined six collected by Harold Cogger of the Australian Museum, and have data on three more collected by Parker and deposited in the Papua New Guinea Museum in Port Moresby (PNGM)—bringing the total for this species to 17.

MATERIAL STUDIED

A total of 27 specimens of *C. siebenrocki* were examined. All specimens, except for SMNS 3991-1 and SMNS 3991-2, were collected by Parker on mainland New Guinea and the offshore island of Daru. The two SMNS specimens were collected by Müller on Saibai Island. MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; AMS = Australian Museum, Sydney; AMNH = American Museum of Natural History, New York; SMNS = Staatliches Museum für Naturkunde, Stuttgart, West Germany.

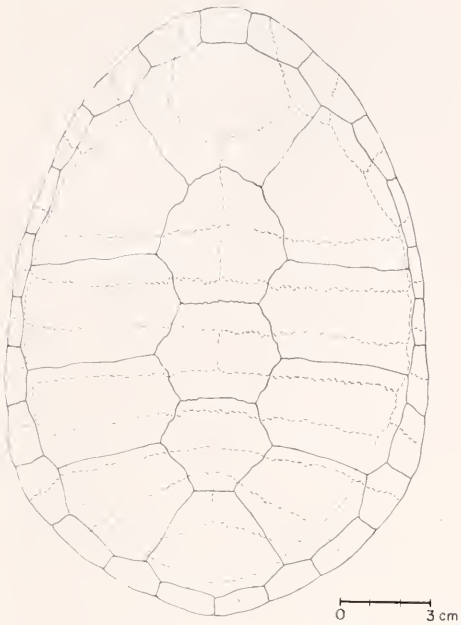

Figure 2. Dorsal view of the carapace of MCZ 134404, a 203 mm female specimen of *C. siebenrocki*. Solid lines indicate scute seams, dotted lines bone sutures.

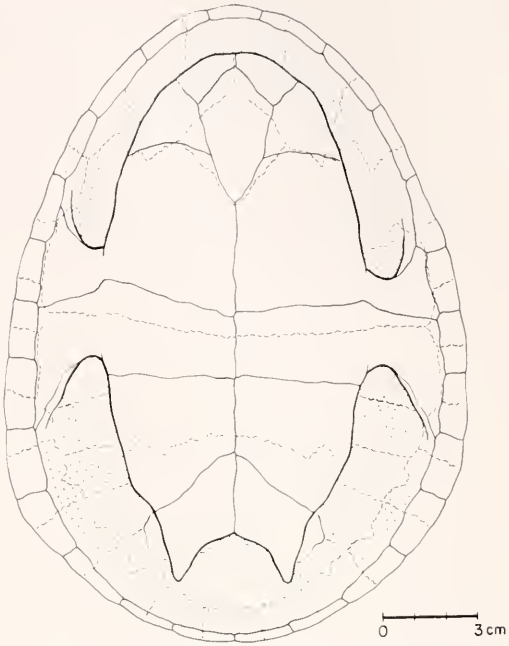

Figure 3. Ventral view of *C. siebenrocki* (MCZ 134404). Note the shape of the anterior plastral lobe and the extent of the anterior ventral marginals.

Balumuk: MCZ 134406, 139551; Boze: MCZ 134466; Daru: MCZ 119721; Dorogori: MCZ 118611; Katatai: MCZ 135397–8, 139541–2, 142496–7, AMNH 111645–6, AMS 40696–7; Mawatta: MCZ 141288; Saibai: SMNS 3991-1, 3991-2; Sigabaduru: MCZ 139547–9; Togo: MCZ 134403–5, 134467–8; Waidoro: MCZ 141694.

Chelodina siebenrocki Werner, 1901
Figures 1–12

Diagnosis. Chelodina siebenrocki is a medium-sized species with a roughly egg-shaped carapace, widening markedly posteriorly but without flaring margins (Fig. 2). The carapace has no keel, is weakly domed, and has a rugose surface and thin scutes. *Anterior ventral marginals*[4] form a very narrow rim between the anterior edge of the carapace and the attachment of skin from the dorsal surface of the neck, so that the ventral surface of the nuchal scute[5] is wider than it is long (Fig. 3). The intergular tends to be long and narrow (Fig. 3). The anal notch is deep and usually semicircular (Fig. 3). The plastron tapers anteriorly and is moderately elongate (not as narrow and long as in *Chelodina oblonga*, not as wide as in *Chelodina longicollis*, Fig. 3). The head is long, wide and relatively flat (flatter than in *C. longicollis*, not as flat as

[4] We have introduced a number of terms new to the chelonological literature, especially for certain skeletal features. These terms are indicated by italics, defined in Appendix I and illustrated in Figs. 3, 4, 5, 6, 8 and 16.

[5] Zangerl (1969) suggests *cervical scute* be used for what most previous authors have called nuchal scute. His reasoning is to avoid confusing the scute and the underlying bone, also called nuchal. Although we otherwise follow Zangerl's terminology, we do not agree with him here. Since there has been little confusion regarding the use of this term, we feel that the introduction of a new term is unnecessary, and simply differentiate between the two "nuchals" by context or add "scute" or "bone."

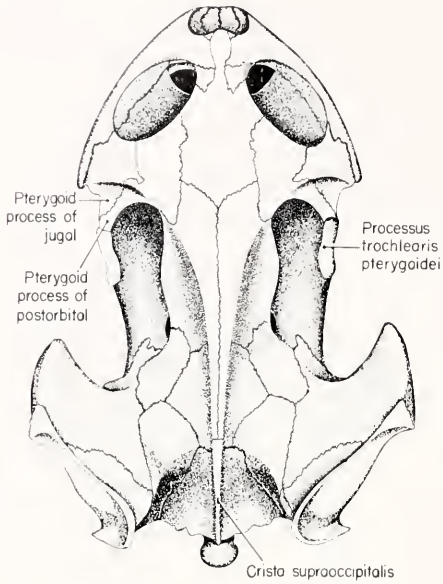

Figure 4. Dorsal view of the skull of *C. siebenrocki* (AMS 40696). The labelled terms include new terms introduced in this paper and defined in Appendix I.

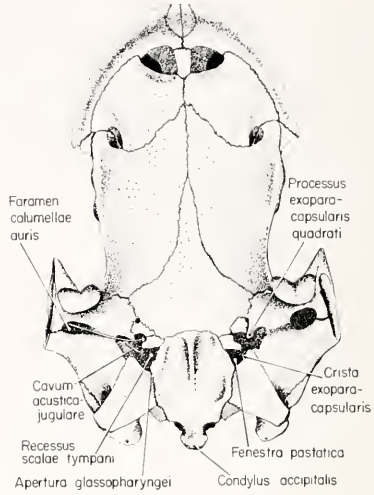

Figure 5. Ventral view of the skull of *C. siebenrocki* (AMS 40696). The labelled terms include new terms introduced in this paper and defined in Appendix I.

Chelodina expansa, Figs. 1, 9). The neck is long and thick (Figs. 1, 9). Coloration is uniform dark brown to black on all dorsal surfaces, uniform yellowish white to tan on all ventral surfaces. The carapace lacks neural bones (Fig. 2). The skull is similar to *C. oblonga*, but the vomer does not usually separate the palatines (Fig. 5). The *prefrontal spine* is relatively prominent (Fig. 6). The hyoid has a clearly defined *crista ventralis hyoideus* (Fig. 8).

EXTERNAL CHARACTERS

Head, neck and limbs. Head flat, broad and elongate, covered on dorsal surface with fine reticulate pattern of skin creases giving the impression of numerous, small, irregularly-shaped scales. Creases absent from tympanum, maxilla, mandible, nasal region and a triangular area along the midline posterior to the orbits (Figs. 1, 9). Chin barbels present, variable in number; often four or more.

Neck long and thick; approximately 75 per cent of length of carapace[6], dorsal surface covered by irregular, flattened tubercles (Figs. 1, 9).

Forelimbs with a single column of transverse, crest-shaped scales on dorsal surface, usually eight; but varying from six to 10. Similar scales on ventral surface of hindlimbs; usually arranged in two columns, with four to six in the medial column and eight to 12 in the lateral column; lateral column extends onto lateral edge of foot and to upper limb; scales rapidly diminish in size as they radiate out towards the foot and the thigh.

Carapace. Carapace roughly egg-shaped, moderately elongate (adult length averaging 1.38 times width; juveniles 1.31 and hatchlings 1.29), fairly flat (length averaging 2.72 times height), widening markedly posteriorly, and with a narrow, pointed anterior portion (Figs. 1, 2, 9). No flaring of marginals either laterally or posteriorly. Supra-anal ridging as in *C. longicollis* also absent. No carapacial keels or tuberculations. No central furrowing along midline of carapace. Weak central depression along

[6] For an explanation of all measurements used in this paper, see Appendix II.

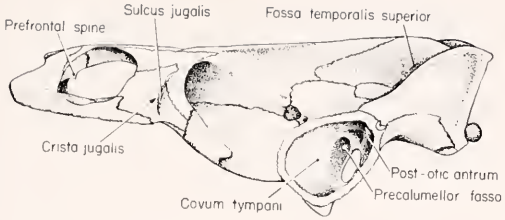

Figure 6. Lateral view of the skull of *C. siebenrocki* (AMS 40696). The labelled terms include new terms introduced in this paper and defined in Appendix I.

midline in very large females. Surface of carapace weakly rugose with reticulate pattern of numerous, very shallow furrows. Furrows on vertebrals oriented longitudinally along midline; furrows on pleurals not oriented in any particular way. Length of dorsal surface of nuchal scute usually greater than width, averaging 1.20 in length: width ratio. All 27 specimens examined had fully formed nuchal scutes. Width of ventral surface of nuchal scute greater than length, averaging 0.42 in length:width ratio (Fig. 3). Anterior ventral marginals form a narrow rim between edge of carapace and attachment of skin from dorsal surface of neck; carapace averages 33.4 times longer than width of second ventral marginal. Width of fifth vertebral greater than length, with the length:width ratio averaging 0.87. Shape of pleurals and first four vertebrals apparently not significant. Twelve marginals on each side of carapace; fifth marginal always in contact with first pleural; eleventh marginal usually in broad contact with fifth vertebral (Figs. 1, 2, 9).

Plastron. Plastron fairly elongate and narrow (Figs. 1, 3). Carapace width averaging 1.87 times plastron width; carapace length averaging 2.53 times plastron width; length of plastron itself averaging 1.89

Figure 7. Medial and slightly ventral view of the right side of the mandible of *C. siebenrocki* (AMS 40696).

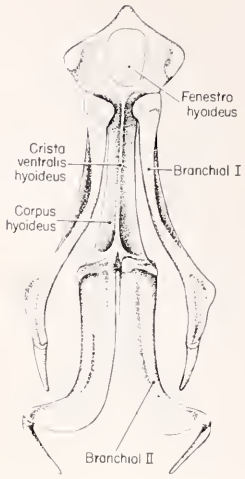

Figure 8. Ventral view of the hyoid of *C. siebenrocki* (MCZ 118611).

times width. Plastron shorter than carapace, with carapace length averaging 1.34 times plastron length (Fig. 3). Anterior lobe generally much narrower than posterior lobe and tapering anteriorly to end in a blunt point (Fig. 3). Tapering less pronounced in large adults. Anal notch deep and semicircular, width averaging 2.25 times depth (Fig. 3). Intergular scute narrow and elongate, length averaging 1.96 times width (Figs. 1, 3). In approximately 15 per cent of specimens examined, the intergular completely separates the gulars and reaches all the way to the anterior plastral margin (as in the type specimen of *Chelodina intergularis* Fry, 1915, which has been synonymized with *C. siebenrocki* by Goode [1967]).

COLORATION

Head, neck and limbs. Color of head uniform dark gray to grayish brown dorsally, grayish white to yellowish ventrally. Neck color dark gray to grayish brown dorsally, dull yellowish white to light yellowish brown ventrally. Limbs and tail dark gray to grayish brown dorsally. Ventral surfaces of feet brown to grayish brown; ventral surfaces of limbs grayish white to

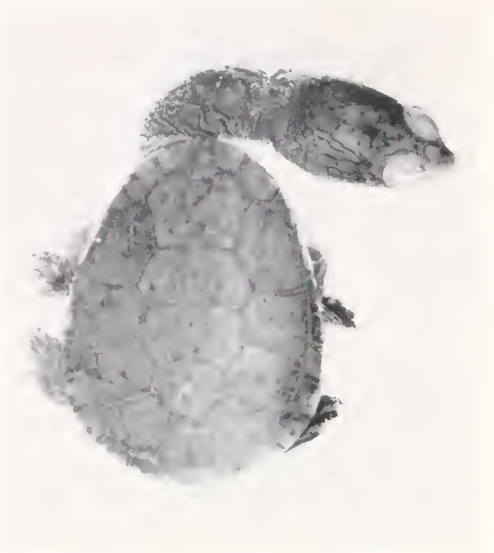

Figure 9. Dorsal view of MCZ 139551, a 37 mm hatchling of *C. siebenrocki*.

light yellowish brown. Soft skin in axillary and inguinal pockets and at base of tail white to light yellowish brown to very light brown.

Carapace. Coloration of dorsal surface of carapace uniform dark brown to black. Coloration of ventral surfaces same color as plastron. Dorsal surface of carapace in hatchlings with fine black spots scattered on dark ground color (Fig. 9).

Plastron. Coloration of plastron uniform light to dark cream or tan; sometimes sutures between scutes finely outlined in dark brown.

Size. Goode (1967) states that *C. siebenrocki* can reach at least 300 mm in carapace length, and Cogger (1972) gives 380 mm as a maximum. Males and females reach approximately the same size; the largest male examined by us was 263 mm, the largest female 273 mm.

Sexual dimorphism. Adult males are distinguished from adult females by tail size and shell height. Adult males have a tail which is considerably longer and thicker than that of females. In our specimens, this difference is apparent only in animals with a carapace length of 150 mm or more, though Bergmans (1966) states that males reach sexual maturity at about 125 mm and females at about 150 mm. Shell height can be used to distinguish males and females over 175 mm in carapace length. Males have a relatively flatter shell than females, with the length:height ratio greater than 2.60. In females, the ratio is less than 2.60. The flatter shell is not due to plastral concavity in male *C. siebenrocki*. No sexual dimorphism is noticeable in shape or depth of anal notch or width of head.

OSTEOLOGY

Skull. Skull moderately elongate, length averaging 1.54 times tympanic width and 1.92 times maxillary width; markedly flattened, with length averaging 6.03 times height, and maxillary width averaging 3.07 times height; narrowed anteriorly, with tympanic width averaging 1.28 times maxillary width. No parietosquamosal connection. Vomer connecting maxillae and palatines, but usually not separating palatines (exception: one of the 12 skulls examined has vomer extending beyond choanal border, separating palatines and reaching anterior edge of pterygoids). Basisphenoid somewhat elongate, length averaging 1.27 times width. Foramen columellae auris on the ventral surface of the skull fairly large and pyriform, with the wider portion laterally located. Processus trochlearis pterygoidei, when viewed from dorsal aspect, makes an approximately 30° angle with the *pterygoid processes of the jugal and postorbital* (Fig. 4). Lateral rim of cavum tympani nearly ovoid, widening slightly anteroventrally. Triturating surfaces of maxillae fairly narrow posterolaterally, contributing only about 13 per cent of skull width at maxillary-pterygoid border. The following features are of importance within cavum acustico-jugulare: recessus scalae tympani entirely open to a large, wide fenestra postotica; small, delicate *processus exoparacapsularis quadrati* barely covers the columella (Fig. 5); crista exoparacapsularis

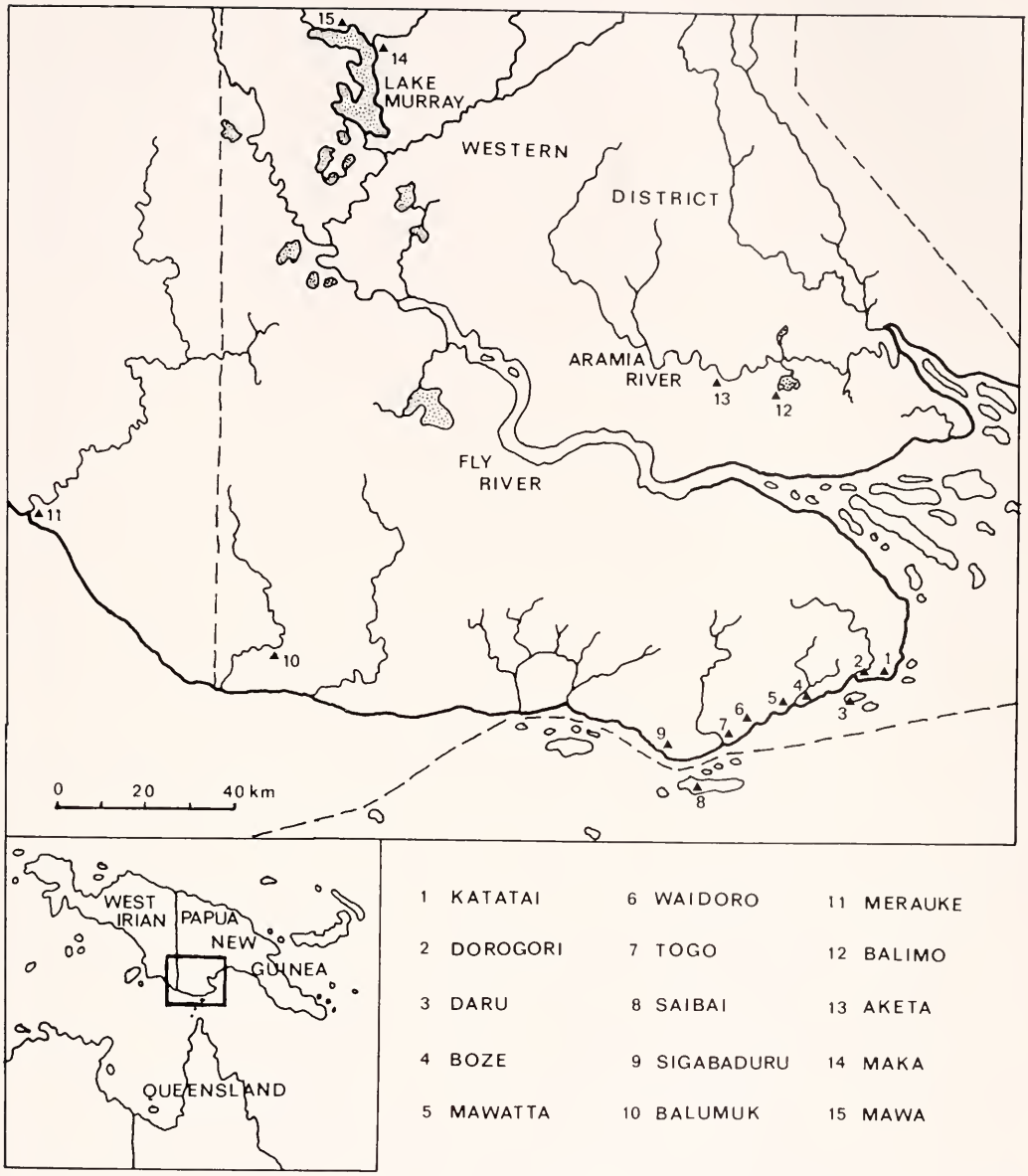

Figure 10. Map of southern New Guinea showing the localities where *C. siebenrocki* and *C. parkeri* have been collected. Localities 1–11 represent *C. siebenrocki*; localities 12–15 are *C. parkeri*.

present only as a weak ridge, dividing the deep medial cavum acustico-jugulare from an extremely shallow or absent lateral fossa; apertura glossopharyngei set close to edge of opisthotic, often present as an incisura in crista exoparacapsularis. Parietals extremely emarginate medially, creating a narrow dorsal surface for attachment of skin. Prefrontals with a well-developed, posteriorly directed spine (*prefrontal spine*—Fig. 6) on the interior anteromedial margin of the orbit. Precolumellar fossa in cavum tympani

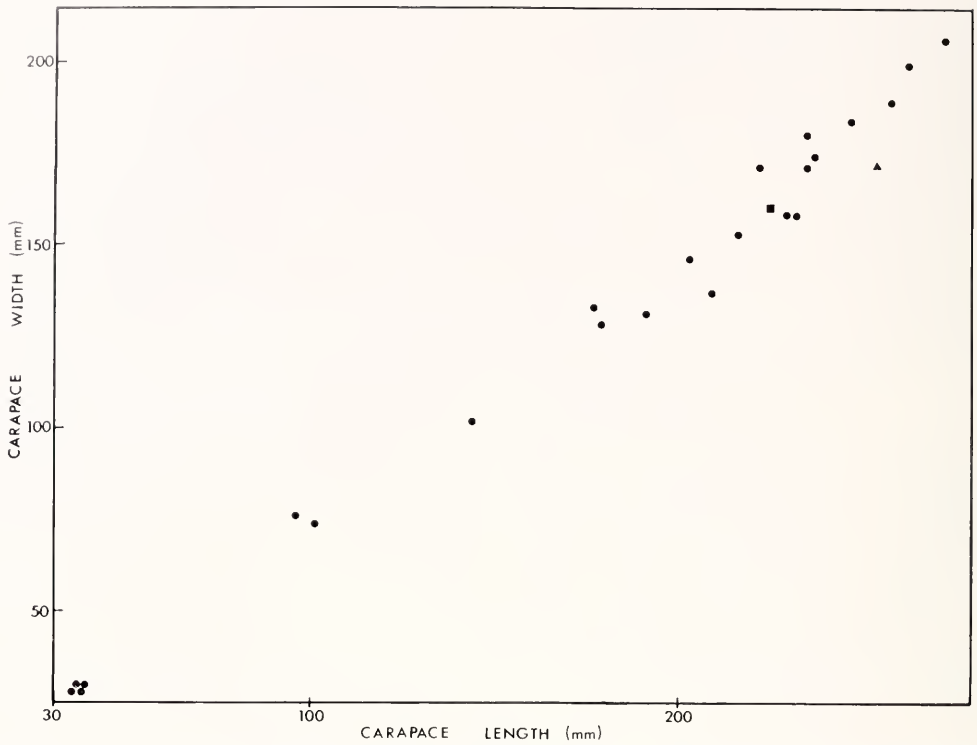

Figure 11. Plot of carapace length vs. carapace width. Solid circles = *C. siebenrocki* specimens discussed in this paper; solid square = type photograph of *C. siebenrocki*; solid triangle = type of *C. rugosa*.

tends to be shallow, ill defined and of the same size or smaller than lateral aspect of foramen columellae auris (Fig. 6). *Sulcus jugalis* (Fig. 6) well-defined; situated posterior to sharp, sometimes overhanging *crista jugalis* (Fig. 6). Columella slender throughout its length, with only slight flattening or flaring at its lateral end. Mandible weak, with a narrow, slanted triturating surface (Fig. 7).

Hyoid. Hyoid very elongate and massive (Fig. 8). Skull length averages 1.78 times length of corpus hyoideus, and carapace length averages 6.09 times length of corpus. Ventral surface of corpus with a well-defined crista ventralis hyoideus (Fig. 8).

Cervical column. Cervical column typical of pattern outlined for all Chelidae by Williams (1950). Data from three specimens indicates that C1 and C7 are amphicoelus, C2, C3 and C4 are opisthocoelus, C5 and C8 are biconvex and C6 procoelus. As pointed out by Williams, this pattern of N(2(,(3(,(4(,(5),)6),)7(,(8) is the only pattern of cervical central articulation known to occur in the Chelidae.

Shell. Carapace with 16 costals (eight on each side), 22 peripherals (11 on each side), nuchal, pygal and suprapygal. Neurals absent. Nuchal bone totally separates first peripherals and partially separates first costals. First peripherals contact first costals (Fig. 2).

Plastron with diamond-shaped entoplastron and paired epiplastra, hyoplastra, hypoplastra and xiphiplastra (Fig. 3).

HATCHLING CHARACTERISTICS

Hatchlings differ in a number of ways from adults and therefore merit separate

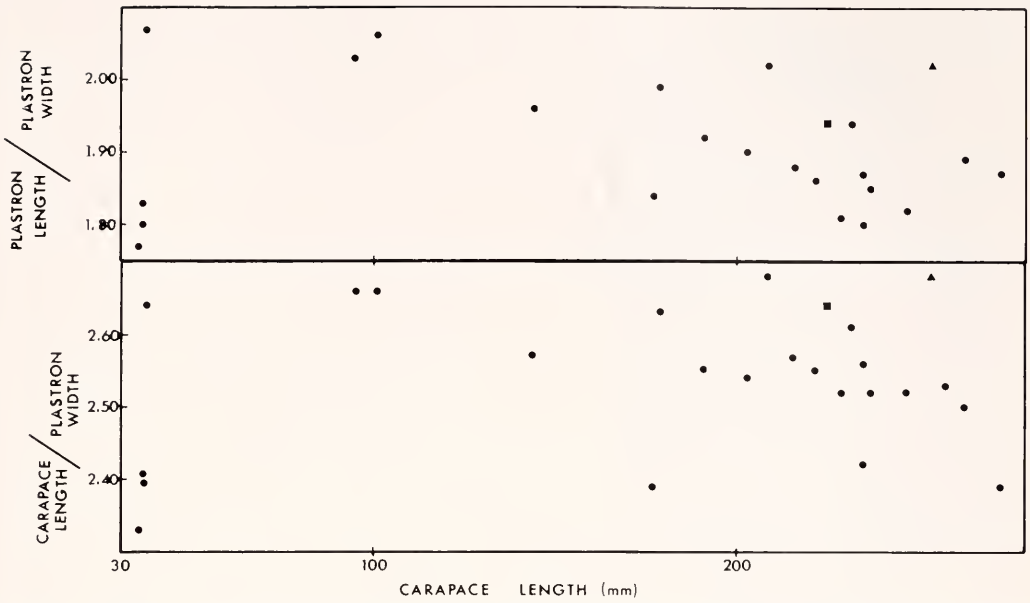

Figure 12. Bottom: Plot of carapace length vs. the ratio of carapace length to plastron width. Top: Plot of carapace length vs. the ratio of plastron length to plastron width. Symbols as in Fig. 11.

discussion here. In general shape of the shell, intergular, dorsal and ventral surfaces of nuchal scute, width of anterior ventral marginal rim and coloration of head and neck, hatchlings agree with adults. However, they differ in a number of other features. The coloration of the carapace differs slightly in hatchlings in that small black spots cover the dark brown surface (Fig. 9). This characteristic was first noted by Siebenrock (1905) in his description of five hatchlings of what he called *C. oblonga* from Saibai Island. The spots vary in number. Each marginal tends to have one, and the vertebrals and pleurals have from zero or one to 10–15 spots each. The width of the head and length of the neck are much greater in relation to carapace length in hatchlings than in adults. During growth, ratios of head length, head width and neck length to carapace length change allometrically and become proportionally much less. Allometric changes in carapace shape include a gradual elongation and decreased posterior widening. The hatchling carapace is also rugose, but longitudinal orientation of furrows occurs on entire surface. The juvenile carapace retains trace of hatchling scute on posteromedial section of each scute and has growth lines radiating out from trace of hatchling scute. The anal notch is deep as in adults, but is more an acute or right angle than a semicircle.

The hatchling skull differs in a number of features from the adult skull. Although length:width ratio is roughly the same as in adults, the maxillary width:height ratio is 1.96, compared to 2.18 in juveniles and 3.07 in adults, and the length:height ratio is 3.38 compared to 4.74 in juveniles and 6.03 in adults—indicating a much flatter skull in adults than in hatchlings. The squamosal extension covering the postotic antrum is shortened and the rim of the cavum tympani is less elongate, being totally circular in the smaller of the two hatchling skulls examined. The precolumellar fossa is poorly defined, but very large and deep and much larger than the foramen columellae auris. The crista supraoccipitalis is short

Figure 13. Dorsal view of MCZ 129897, a 136 mm specimen of *C. parkeri*. Note especially the vermiculate pattern on the head, the reticulate pattern on the carapace, the general shape of the carapace and the reduced triangular dorsal surface of the nuchal scute.

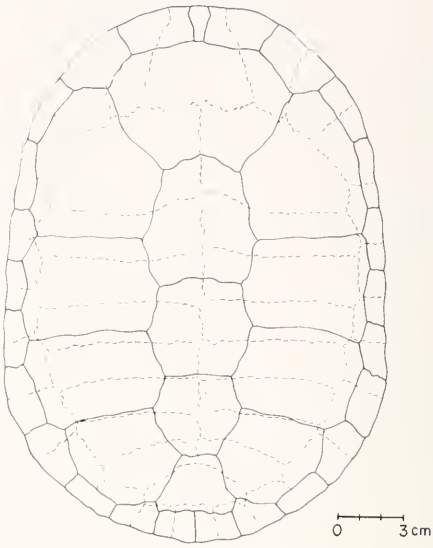

Figure 14. Dorsal view of the carapace of MCZ 134400, a 257 mm female specimen of *C. parkeri*. Solid lines indicate scute seams, dotted lines bone sutures.

and flat, resulting in a very shallow fossa temporalis superior and a relatively enlarged parietal surface on top of the skull. The basisphenoid has its characteristic shape, as does the vomer, which as in most adults, does not separate the palatines. The prefrontal spine is present. The quadrate does not completely encircle the cavum tympani, leaving a notch in its ring at the site of the incisura columellae auris. The basioccipital is poorly developed but markedly biconcave. The hyoid has a rounded, not angulated, corpus, with no crista ventralis hyoideus. In general, the skull of hatchling *C. siebenrocki* is similar in degree of flattening to adults of group A species (Burbidge, et al., 1974), but becomes considerably flatter during the course of growth.

DISTRIBUTION AND ECOLOGY

Distribution. *C. siebenrocki* is apparently restricted to the tidal portions of the small streams flowing to New Guinea's south coast, and to tidally-influenced coastal swamps and offshore islands such as Daru and Saibai (F. Parker, personal communication, 1973). Collecting localities which we have verified by examining specimens are restricted to the coastal areas of the low-lying marsh country to the south of the Fly River (Fig. 10). All collecting localities are in the Papua New Guinea Western District, with the exception of Saibai Island. There is also a reliable literature record for *C. siebenrocki* from Boeti, near Merauke in West Irian (Bergmans, 1963, 1966). We are not sure if *C. siebenrocki* occurs on the Cape York Peninsula of Australia. We follow Burbidge (1967) and Burbidge, et al. (1974) in considering *C. siebenrocki* distinct from *C. rugosa* of Cape York, but the relationship between these two species requires further investigation. Werner's type locality of German (now Northeast)

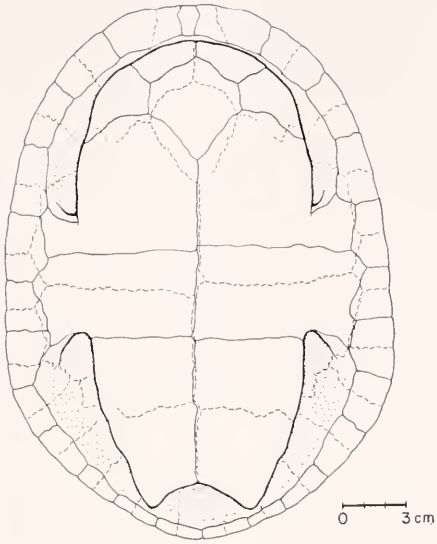

Figure 15. Ventral view of *C. parkeri* (MCZ 134400). Note especially the shape of the anterior plastral lobe and the extent of the anterior marginals.

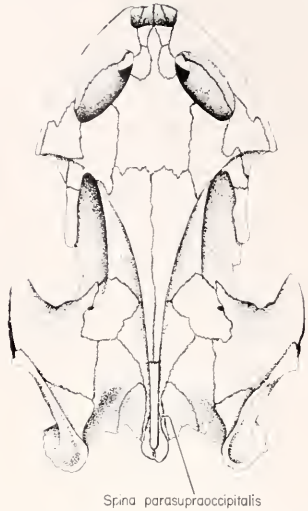

Figure 16. Dorsal view of the skull of *C. parkeri* (AMS 21434). Note the location of the spina parasupraoccipitalis.

New Guinea is probably incorrect, since no specimens of *Chelodina* are known from north of the Central Ranges (Brongersma, 1958, 1961; Cogger, 1972). The only chelid turtle which appears to inhabit Northeast New Guinea is *Elseya novaeguineae* (Brongersma, 1961; Cogger, 1972).

Ecology. Little is known of the habits of *C. siebenrocki.* It does not bask, but spends most of its time on and in deep, soft mud characteristic of the south coast (Parker, personal communication, 1974). It is usually caught by feeling around with bare feet in the mud. It is not an aggressive animal and will not bite even when handled. Local villagers in New Guinea do not eat it, although *Emydura subglobosa* and *Elseya novaeguineae* are readily eaten and sold at markets (Parker, personal communication, 1974). It is apparently carnivorous, using its long neck to strike for food (Bergmans, 1966).

C. siebenrocki appears to breed seasonally, laying eggs at the end of the wet season in May, which hatch at the start of the next wet season in November or December (Parker, personal communication, 1974). Copulation takes place in the water, with the male mounting the female from behind (Bergmans, 1966). The female leaves the water to lay her eggs in a nest which she digs in the available substratum. Bergmans (1966) figures a 95 mm deep nest dug by a captive female. It has an unusual shape, cylindrical in the upper half, but bulging out to one side at the base (Bergmans, 1966). Two egg clutches collected by Parker at Katatai had 17 and four eggs. The average size of the eggs in the larger clutch was 35.0 × 28.25 mm, and in the smaller clutch 36.1 × 28.9 mm. An attempt at artificial incubation yielded an 18 mm embryo after 187 days, and a 28 mm embryo after 272 days (Parker, personal communication, 1974). Although no fully developed hatchlings resulted from this attempt, a linear extrapolation to 35 mm results in an estimated incubation time of 330 days. This unusually long incubation period may result from the artificial conditions. However, at least one other *Chelodina*, *C. expansa*, has an incubation period that normally exceeds 324 days (Goode and Russell, 1968).

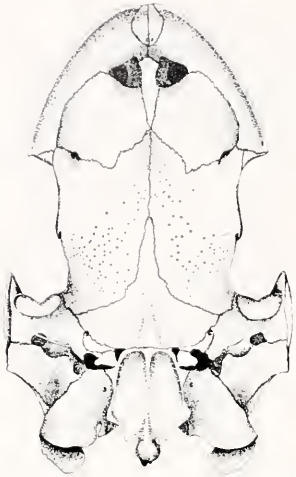

Figure 17. Ventral view of the skull of *C. parkeri* (AMS 21434).

Figure 18. Lateral view of the skull of *C. parkeri* (AMS 21434).

Hatching under natural conditions appears to occur at a carapace length of about 35 mm. A recent hatchling caught by Parker at Sigabaduru on January 17 measured 36 mm, while another from Balumuk, caught on February 19, measured 37 mm.

C. siebenrocki apparently occurs sympatrically with *Chelodina novaeguineae*, *Emydura subglobosa* and *Elseya novaeguineae*, and possibly *Carettochelys insculpta* and *Pelochelys bibroni*.

DISCUSSION

Nomenclature. The major nomenclatorial problem involving *C. siebenrocki* has resulted from the belief that *Chelodina oblonga*, a distinct species endemic to southwestern Australia, extends as far north as northern Australia and islands south of New Guinea. Gray (1844) referred a specimen from Port Essington (Darwin) in the Northern Territory of Australia to *C. oblonga*, while Strauch (1890) and Schenkel (1901) added to the confusion by reporting *C. oblonga* from Prince of Wales Island and Thursday Island, both in the Torres Strait near the northern Australian coast. These three localities are all within the range of *C. rugosa*. Finally, Siebenrock (1905) referred five embryos of *C. siebenrocki* from Saibai Island near the coast of New Guinea to *C. oblonga*. Most later authors (Werner, 1909; Siebenrock, 1909; DeRooij, 1915; Loveridge, 1948; Mertens and Wermuth, 1955; Wermuth and Mertens, 1961; Mehrtens, 1967) recognized *C. siebenrocki* as a distinct species from mainland New Guinea, but followed the error of earlier authors by citing *C. oblonga* from northern Australia and islands in the Torres Strait.

Siebenrock (1915) synonymized *C. siebenrocki* with *C. oblonga*, after already having synonymized *C. rugosa* with *C. oblonga* in 1909.

Goode (1967) considers *C. rugosa* of northern Australia and *C. siebenrocki* of New Guinea to be conspecific and refers to both as *C. siebenrocki*, although the name *C. rugosa* Ogilby, 1890 has priority over *C. siebenrocki* Werner, 1901.

Blackmore (1969) considers *C. siebenrocki* only subspecifically distinct from *C. oblonga*.

Burbidge (1967) and Burbidge, et al. (1974) are the first to assert that *C. oblonga* does not occur in northern Australia and on the Torres Strait Islands, but is endemic to southwestern Australia and clearly distinct from *C. siebenrocki* and *C. rugosa*.

Peters (1969) mentions *C. siebenrocki* from Cooktown on the Cape York Peninsula, but his specimens are probably referable to *C. rugosa*.

Cogger (1972) discusses *C. siebenrocki* from New Guinea. However, his description and the accompanying photograph are of the new species, *Chelodina parkeri*, and not of *C. siebenrocki*.

Figure 19. Medial and slightly dorsal view of the right side of the mandible of *C. parkeri* (AMS 21434).

Other authors mentioning *C. siebenrocki* include Ogilby (1905), Stejneger (1909), Loveridge (1934) and Pritchard (1967).

Relationships with C. rugosa and other species. The series of *C. siebenrocki* described in this paper shows little phenotypic variation. The greatest variation within the series is found in a single specimen (MCZ 134406), which has a vomer that separates the palatines and a very wide head. Large, wide heads occasionally occur in adult specimens of some other Australian chelids (Worrell, 1963), and may also in *C. siebenrocki*. The differences exhibited by MCZ 134406 are probably best explained in this way.

C. siebenrocki is most closely related to *C. rugosa*, with which it may be synonymous, although Burbidge (1967) and Burbidge, et al. (1974) believe that it is distinct. The relationship between these animals remains unclear. We have compared the New Guinean series discussed here with the type specimen of *C. rugosa* and with a series of seven specimens from the Cape York Peninsula of northern Australia that have been referred to *C. rugosa* on the basis of locality. The type specimen of *C. rugosa* is only a shell (carapace and plastron). Although it has a slightly narrower carapace and plastron (Figs. 11, 12), it agrees in most respects with the New Guinean series and the type photographs of *C. siebenrocki*. The seven Cape York specimens are quite variable compared to the New Guinean series, and the sample is too small to permit any conclusions concerning specific status to be drawn. For the present, we prefer to simply refer to all *C. rugosa*-like turtles (including *C. siebenrocki*) from northern Australia and New Guinea as the *C. rugosa* complex, and defer final judgment on the relationship between *C. rugosa* and *C. siebenrocki* until more adequate material from northern Australia becomes available.

Figure 20. Ventral view of the hyoid of *C. parkeri* (AMS 21353).

C. siebenrocki is also closely related to the new species which we are describing. It is less closely related to *C. oblonga* of southwestern Australia and *C. expansa* of southeastern Australia. It is distinguished from *C. oblonga* by the absence of neurals (*C. oblonga* being the only *Chelodina* with neural bones [Burbidge, 1967; Burbidge, et al., 1974]), the shorter vomer which rarely extends posteriorly to separate the palatines, the presence of a prefrontal spine, and the less elongate shell. It is distinguished from *C. expansa* by the higher skull, the prefrontal spine, the narrower carapace, the narrower, tapering plastral lobe, the narrow rim of anterior ventral marginals, and the smaller maximum size (*C. expansa* reaches a length of 423 mm [Goode, 1967]).

Chelodina parkeri sp. nov.
Figures 10, 13–24

Holotype: AMS 21425, Mawa, Lake Murray, Western District, Papua New Guinea, collected November 7, 1963 by Harold Cogger.

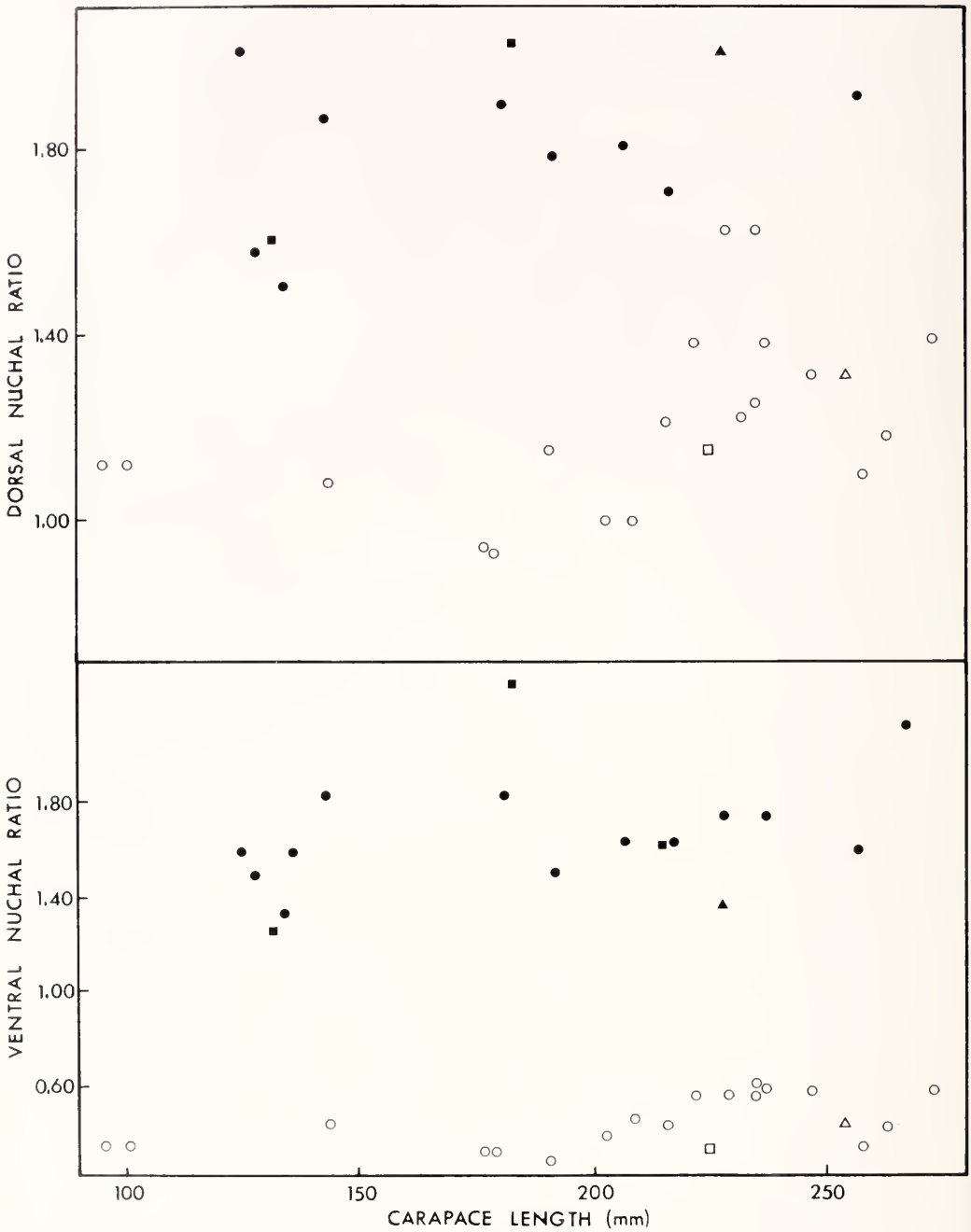

Figure 21. Bottom: Plot of carapace length vs. the ratio of length to width of the ventral surface of the nuchal scute. Top: Plot of carapace length vs. the ratio of length to width of the dorsal surface of the nuchal scute. (Specimens with triangular nuchals are not plotted.) Solid circles = paratypes of *C. parkeri*; solid triangle = holotype of *C. parkeri*; solid squares = specimens of *C. parkeri* from the Papua New Guinea Museum (measurements provided by Fred Parker); open circles = specimens of *C. siebenrocki* discussed in the first part of this paper; open square = type photograph of *C. siebenrocki*; open triangle = type specimen of *C. rugosa*.

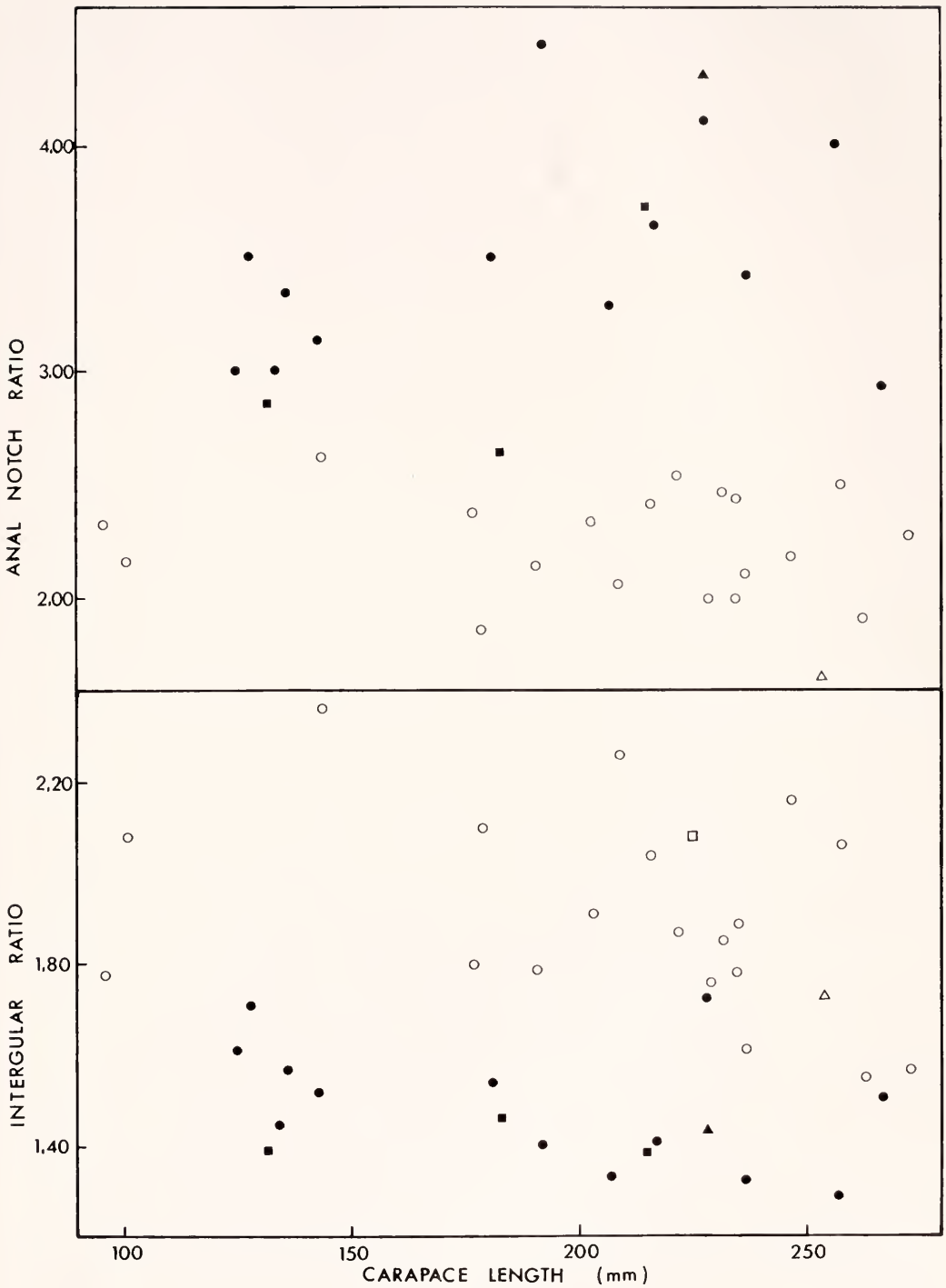

Figure 22. Bottom: Plot of carapace length vs. the ratio of length to width of the intergular scute. Top: Plot of carapace length vs. the ratio of width to depth of anal notch. Symbols as in Fig. 21.

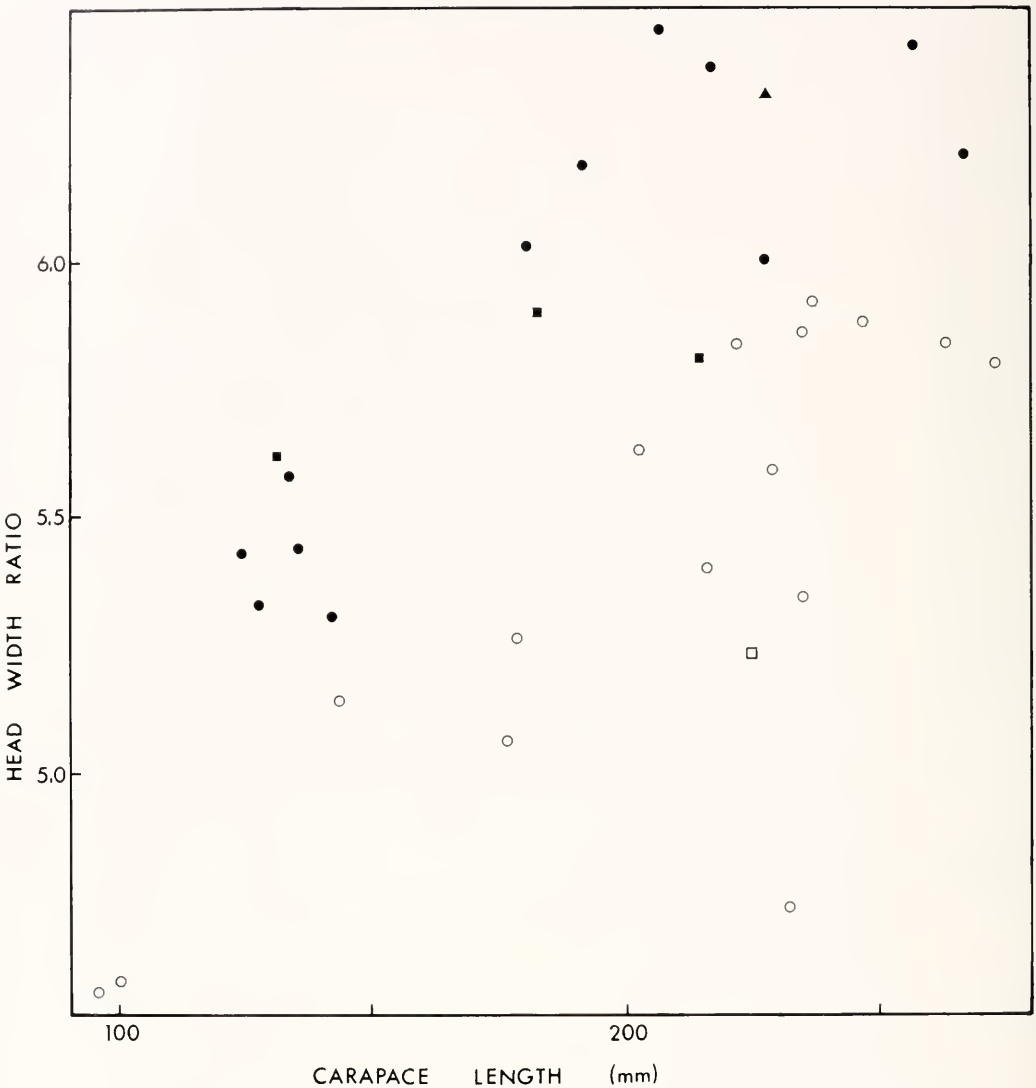

Figure 23. Plot of carapace length vs. the ratio of carapace length to head width. Symbols as in Fig. 21.

Paratypes: MCZ 119722, 119723, Balimo, Western District, Papua New Guinea, collected November 7, 1967 by Fred Parker; MCZ 129897, 134400, Maka, Lake Murray, Western District, Papua New Guinea, collected June 7, 1969 by Fred Parker; MCZ 134401, Maka, Lake Murray, collected July 23, 1969 by Fred Parker; MCZ 134402, Balimo, collected March 14, 1969 by Fred Parker; MCZ 134464, Maka, Lake Murray, collected November 6, 1969 by Fred Parker; MCZ 134465, Maka, Lake Murray, collected November 22, 1969 by Fred Parker; AMS 21159, Aketa, Aramia River, Western District, Papua New Guinea, collected October 31, 1963 by Harold Cogger; AMS 21423–4, Mawa, Lake Murray, collected November 7, 1963 by Harold Cogger; AMS 21353, 21434, Balimo, collected October 29, 1963 by Harold Cogger.

In addition to the type series, Parker (personal communication, 1974) has provided us with information on three specimens in the Papua New Guinea Museum (PNGM R1225, Balimo, collected March 14, 1969 by Fred Parker; PNGM R1601,

Maka, Lake Murray, collected November 6, 1969 by Fred Parker; PNGM 11635, Maka, Lake Murray, collected January, 1973).

We are pleased to name this new species in honor of Fred Parker and in recognition of his many superb collections which have contributed so much to our knowledge of New Guinean herpetology.

Diagnosis. *Chelodina parkeri* is a medium-sized species closely resembling *C. siebenrocki*, but distinguished by the color pattern on the head which is unique within the genus *Chelodina* (Fig. 13). The entire dorsal surface of the head and the mandible are extensively vermiculated with white, yellow or pale green lines and dots on a dark brown background, while a larger, brighter, more prominent blotch is present posteromedial to each tympanic membrane. This color pattern is retained in adult animals, although the pattern is faded in some specimens. The carapace is similar to *C. siebenrocki*, though it is not as egg-shaped and has more nearly parallel sides with a less expanded posterior margin and a wider anterior margin (Figs. 14, 15). Juveniles and subadults have vertebral tuberculations which disappear with age. Hatchlings of *C. parkeri* are unknown at the present time. The plastron is moderately elongate and tends to have a wide, truncate, anterior lobe (Fig. 15). The anterior ventral marginals form a wide margin between the edge of the carapace and the dorsal skin attachment, so that the ventral surface of the nuchal scute is longer than it is wide (Fig. 15). The intergular is not greatly elongate, and tends to be shorter and wider than in *C. siebenrocki* (Fig. 15). The anal notch is shallow and triangular (Fig. 15); the neck long and thick (Fig. 13). The head is long, wide and relatively flattened (Fig. 13). The coloration of the carapace differs from *C. siebenrocki*, being lighter brown, often with indistinct pale yellow reticulations mainly along anterior and posterior margins, but also at times covering the entire carapace (Fig. 13). The plastron is dull yellow and has no pattern. There are no neural bones in the carapace (Fig. 14).

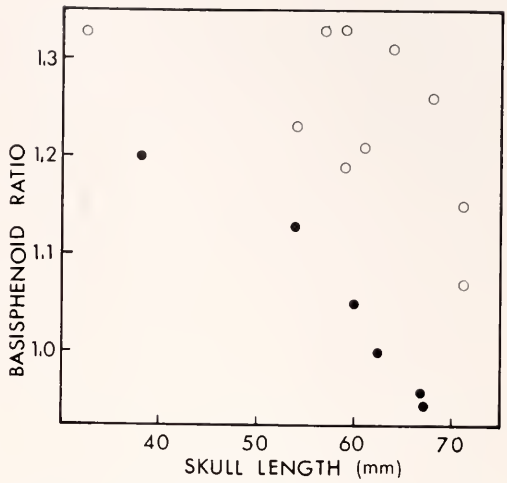

Figure 24. Plot of skull length vs. the ratio of length to width of the basisphenoid bone. Symbols as in Fig. 21.

The skull is similar to *C. siebenrocki*, but the vomer separates the palatines (Fig. 17); a prefrontal spine is absent (Fig. 18), and a *spina parasupraoccipitalis* is present to varying extent (Fig. 16). The hyoid does not have a sharp crista ventralis hyoideus, but instead a more obtusely-angulated corpus hyoideus (Fig. 20).

EXTERNAL CHARACTERS

Head, neck and limbs. Head elongate, flattened and wide, though narrower than in *C. siebenrocki* (Figs. 13, 23); covered on the dorsal surface with a fine, reticulate pattern of skin creases which give the impression of numerous, small, irregularly-shaped scales. Creases absent from tympanum, maxilla, mandible, nasal region and a triangular area along the midline posterior to the orbits. Variable number of chin barbels present, but usually only two and of smaller size than in *C. siebenrocki*.

Neck long and thick, averaging about 75 per cent of carapace length, and covered on dorsal surface with very small, pointed, well-defined tubercles set closely together (Fig. 13).

Transverse scales on forelimbs usually seven in one column, but varying from six to nine. Transverse scales on hindlimbs usually five to seven medially and eight to 11 laterally in double column similar to *C. siebenrocki*.

Carapace. Carapace moderately elongate (adult length averaging 1.43 times width, juveniles length 1.38 times width), fairly shallow, length averaging 2.59 times height, and having nearly parallel sides with only a slight expansion at the posterior margin, and a wide, truncate anterior margin (Figs. 13, 14). No flaring of the margins, no supra-anal ridging, no keels, and no central furrowing. Broad, flattened tuberculations on third, fourth and fifth vertebrals in larger juveniles and subadults up to a carapace length of about 150 mm, after which the tuberculations gradually disappear or are worn off, leaving the adult shell evenly domed. It is not known if hatchlings and small juveniles possess these tuberculations since no specimens under 125 mm have been collected. Surface of carapace smooth, with generally thinner scutes than *C. siebenrocki* and a similar but shallower pattern of rugosities. Juvenile scute pattern same as in *C. siebenrocki*, with hatchling shields retained, and a radiating pattern of growth ridges and rings. These hatchling scutes eventually peel off to reveal the rugose adult pattern. Dorsal surface of nuchal scute narrow and elongate, length averaging 1.80 times width when fully present. Approximately 30 per cent of specimens possess reduced triangular nuchals which do not totally separate the first marginals and do not contact the first vertebral. None of the specimens examined entirely lacked the nuchal. Length of ventral surface of nuchal scute greater than width, length averaging 1.66 times width and always fully present. Anterior ventral marginals form a wide margin between edge of carapace and dorsal skin attachment, with carapace length averaging only 15.5 times the width of the second ventral marginal (Fig. 15). Length of fifth vertebral greater than width, with the length:width ratio averaging 1.23. Shape of pleurals and first four vertebrals apparently not siginificant. Twelve marginals present; fifth marginal always in contact with first pleural; eleventh marginal usually in narrow contact or not in contact with fifth vertebral (Figs. 13, 14).

Plastron. Plastron fairly elongate and moderately narrow, with carapace width averaging 1.73 times plastron width, carapace length averaging 2.45 times plastron width, and plastron length itself averaging 1.90 times its width (Fig. 15). Plastron shorter than carapace, with carapace length averaging 1.28 times plastron length (Fig. 15). Anterior lobe generally as wide as or wider than posterior lobe, ending anteriorly in a broad, truncate manner (Fig. 15). Anal notch shallow and triangular, width averaging 3.46 times depth (Fig. 15). Intergular not markedly elongate, tending to be shorter and wider than in *C. siebenrocki*, length averaging 1.48 times width (Fig. 15). In none of the specimens examined does the intergular reach the anterior plastral margin.

COLORATION

Head, neck and limbs. *C. parkeri* is the only member of the genus *Chelodina* that has a light color pattern on its head. In juveniles, the reddish brown to brown ground color on the dorsal surface of the head and the mandible is covered with bright yellow vermiculations made up of irregular, though sharply outlined, lines and dots (Fig. 13), with a larger, whiter, more prominent blotch posteromedial to each tympanic membrane. Ground color of adult head grayer, with white, yellow or pale green vermiculations on dorsal surfaces and white vermiculations on mandible. Adult head markings similar to but sometimes less sharply demarcated than those of juveniles. Occasional specimens have a very faded head pattern, but the pattern is always present to some extent. Color of vermiculations fades to pale grayish white in preserved specimens. Adult eye

color brown, with a narrow but distinct ring of yellow rimming free edge of iris.

Dorsal surfaces of limbs and neck gray; ventral surfaces grayish white, sometimes with pinkish tint.

Carapace. Ground color of carapace brown to dark brown, though in general lighter than in *C. siebenrocki.* Pale yellow reticulations of irregular shape usually present as a thin band along anterior and posterior margins of carapace, but may vary in extent from totally absent to covering entire carapace. Intensity and extent of reticulations apparently not age-related. Ventral surfaces of carapace same color as plastron.

Plastron. Coloration of plastron uniform pale yellow.

Size. The largest specimen of *C. parkeri* measured was a 267 mm female. The largest male measured 217 mm. It is possible that this disparity indicates some sexual dimorphism in size, but it is more likely the result of absence of large males from the small sample analysed.

Sexual dimorphism. Sexual dimorphism is similar to that of *C. siebenrocki*, with mature males over 150 mm having larger tails and flatter shells than females. The flatter shell in males is not due to plastral concavity. A length:height ratio of greater than 2.60 characterizes a male, as in *C. siebenrocki.*

OSTEOLOGY

Skull. Skull moderately elongate, length averaging 1.63 times tympanic width and 2.00 times maxillary width; skull also markedly flattened, with length averaging 6.20 times height, and maxillary width averaging 3.14 times height; skull narrowed anteriorly, with tympanic width averaging 1.23 times maxillary width (Figs. 16, 17, 18). No parietosquamosal connection (Fig. 18). Vomer connecting maxillae and palatines, separating palatines along most of their length and usually reaching the anterior border of the pterygoids (Fig. 17). Basisphenoid as wide as long, with the length: width ratio averaging 1.02 (Fig. 17). Foramen columellae auris on the ventral skull surface fairly small and rectangular or slitlike (Fig. 17). Processus trochlearis pterygoidei, when viewed from dorsal aspect, continues as a straight extension of pterygoid processes of jugal and postorbital, not making an angle with them as in *C. siebenrocki* (Fig. 16). Lateral rim of cavum tympani elongate, flattened and pyriform, with the wider aspect located anteroventrally (Fig. 18). Triturating surfaces of maxillae fairly wide posterolaterally, contributing about 20 per cent of skull width at maxillary-pterygoid border (Fig. 17). The following features are of importance within cavum acustico-jugulare: recessus scalae tympani nearly completely roofed over by basioccipital and opisthotic and only narrowly open to a small fenestra postotica; substantial though delicate processus exoparacapsularis quadrati covers the columella; crista exoparacapsularis present as a sharp ridge, dividing cavum acustico-jugulare into two deep fossae, a medial one for the paracapsular sac and a lateral one for the vena capitis lateralis and columellar artery; apertura glossopharyngei fully penetrating opisthotic, never present as an incisura in crista exoparacapsularis (Fig. 17). Parietals considerably emarginate medially, though not quite as extensively as in *C. siebenrocki* (Fig. 16). Prefrontals lack the prefrontal spine which is characteristic of *C. siebenrocki*, but supraoccipital has a spinous process (spina parasupraoccipitalis, Fig. 16) extending posteriorly along dorsal surface of exoccipital in a specific sulcus. Spina parasupraoccipitalis varies considerably in length, being no more than an indistinct spur in some specimens, but reaching the posterior skull border and giving the impression of a split exoccipital in others. Precolumellar fossa tends to be deep, well-defined and of the same size or slightly larger than lateral aspect of foramen columellae auris (Fig. 18). Sulcus jugalis poorly developed and shallow, situated posterior to a weak crista jugalis (Fig. 18).

Columella less slender than in *C. siebenrocki* and greatly flattened and flared out at its lateral end. Mandible weak, with a wide, partly horizontal triturating surface (Fig. 19).

Hyoid. Hyoid elongate and massive, structurally very similar to *C. siebenrocki.* Skull length averages 1.65 times length of corpus hyoideus, and carapace length averages 6.25 times length of corpus. Long ventral surface of corpus without a sharp crista ventralis hyoideus, but rather a very weak ridge that creates an approximate right angle along the shaft of the corpus hyoideus (Fig. 20).

Cervical column. The pattern of central cervical articulation for three specimens examined for this character is N(2(,(3(,(4(,(5),)6),)7(,(8), which is identical to all Chelidae previously described (Williams, 1950).

Shell. Carapace with 16 costals (eight on each side), 22 peripherals (11 on each side), nuchal, pygal and suprapygal (Fig. 14). Neurals absent. Nuchal bone totally separates first peripherals, but does not separate first costals. First peripherals contact first costals.

Plastron with diamond-shaped entoplastron and paired epiplastra, hyoplastra, hypoplastra and xiphiplastra (Fig. 15).

DISTRIBUTION AND ECOLOGY

Distribution. *C. parkeri* is apparently endemic to New Guinea, being restricted to the large inland grass swamps surrounding Lakes Murray and Balimo and the Fly and Aramia Rivers (Parker, personal communication, 1973). Verified collection localities are restricted to the Western District's savanna regions north of the Fly River (Fig. 10).

Ecology. *C. parkeri* appears to inhabit the open edges of lakes and rivers, where a dense growth of grass and aquatic vegetation floats on the shallow water (Parker, personal communication, 1973; Cogger, personal communication, 1974). The lagoons where it is found are subject to periodic inundation and partial or complete drying during exceptionally dry seasons (Cogger, 1964; Parker, personal communication, 1973). Most specimens were collected in muddy streamside shallows by feeling around in the mud with bare feet, although some animals were also taken with nets in shallow water (Cogger, personal communication, 1974). In captivity, *C. parkeri* is apparently exclusively piscivorous (Sachsse, personal communication, 1974).

C. parkeri shares its habitat with large numbers of *Emydura subglobosa* (Cogger, personal communication, 1974), but is itself rather rare (Parker, personal communication, 1973). It apparently also occurs sympatrically with *Chelodina novaeguineae*, *Elseya novaeguineae*, *Carettochelys insculpta* and possibly *Pelochelys bibroni.* It is nowhere sympatric with the exclusively coastal *C. siebenrocki.*

DISCUSSION

Relationships with C. siebenrocki and other species. *C. parkeri* is a *Chelodina* group B turtle (Burbidge, et al., 1974). It is most closely related to *C. siebenrocki* and *C. rugosa* and less closely related to *C. expansa* and *C. oblonga.* The major distinguishing features of *C. parkeri* are the head color pattern and the shape of the ventral surface of the nuchal scute. *C. parkeri* is the only member of the genus *Chelodina* which has any kind of light color pattern on the dorsal surface of the head and this criterion is usually enough to differentiate it. However, in some specimens, the head color pattern is so faded that other criteria must also be used. The lack of neural bones and the wider carapace and plastron separate *C. parkeri* from *C. oblonga.* It is distinguished from *C. expansa* by its higher skull, narrower carapace and smaller maximum size. The elongate ventral surface of the nuchal scute is the most useful character (aside from head coloration) for separating *C. parkeri* from specimens of the *C. rugosa* complex (including *C. siebenrocki*). Members of the *C. rugosa*

complex invariably have a nuchal scute with a very wide ventral surface (Fig. 21). Correlated with this feature, the anterior ventral marginals form a wide rim in *C. parkeri* and a narrow rim in members of the *C. rugosa* complex.

There are several other differences between *C. parkeri* and the *C. rugosa* complex which are helpful but not necessarily by themselves sufficient to distinguish the species. The most important of these are the prefrontal spine, the vomer, the spina parasupraoccipitalis and the vertebral tuberculations. The prefrontal spine is always absent in *C. parkeri*, always present in *C. siebenrocki* and almost always present in *C. rugosa* (a single specimen from the Kimberly Plateau in Western Australia lacks this spine). The vomer separates the palatines and reaches the pterygoids in *C. parkeri*, but only rarely (one out of 12 skulls) does so in *C. siebenrocki*. The size of the vomer in *C. rugosa* is variable; some individuals have a *C. parkeri*-like vomer and others a shorter one of the *C. siebenrocki* type. The spina parasupraoccipitalis is always absent in members of the *C. rugosa* complex and always present in *C. parkeri*, though it varies greatly in size and is sometimes very small. Vertebral tuberculations are present in juvenile and subadult (and possibly also hatchling) *C. parkeri*, but never in *C. siebenrocki*.

Finally, there are a host of less important and more variable features which help distinguish *C. parkeri* from *C. siebenrocki*, but which must be used in combination with other more important characters. The dorsal surface of the nuchal scute is generally longer and narrower in *C. parkeri*, but there is some overlap with *C. siebenrocki* (Fig. 21). The anal notch is not as deep in *C. parkeri* (Fig. 22). The intergular is not as elongate in *C. parkeri* (Fig. 22). The fifth vertebral tends to be longer and narrower in *C. parkeri*. The sides of the carapace in *C. parkeri* are more nearly parallel and often have reticulations along the edge. The anterior plastral lobe in *C. parkeri* tends to be more truncate and wider. The head is narrower in relation to carapace length in *C. parkeri* (Fig. 23). The basisphenoid is wider and shorter in *C. parkeri* (Fig. 24). The foramen columellae auris is more rectangular than oval in *C. parkeri*. The processus trochlearis pterygoidei forms a straight, rather than angulated continuation of the pterygoid processes of the jugal and postorbital in *C. parkeri*. The rim of the cavum tympani is more elongate and pyriform in *C. parkeri*. The triturating surface of the maxillae is wider. The parietals are not as extensively medially emarginate in *C. parkeri*. The precolumellar fossa tends to be deeper and better defined in *C. parkeri*. The sulcus jugalis and crista jugalis are less developed in *C. parkeri*. The recessus scalae tympani is more roofed over and less open to the fenestra postotica. The processus exoparacapsularis quadrati is slightly larger in *C. parkeri*. The crista exoparacapsularis creates a deep lateral fossa rather than a shallow one. The apertura glossopharyngei is more completely enclosed by the opisthotic in *C. parkeri*. The hyoid lacks a crista ventralis hyoideus in *C. parkeri*. The columella in *C. parkeri* has a wider, more flared lateral end. The mandible has a more horizontal triturating surface in *C. parkeri*.

Additional comments. *C. parkeri* is apparently not only endemic to New Guinea, but is also restricted to inland areas on the southern part of the island. It does not occur in the coastal region of southern New Guinea and is thus isolated from access to the Torres Strait, an apparent "cross-over" route for fauna of northern Australia and southern New Guinea. All other New Guinean chelid turtles, and also the cryptodire *Carettochelys insculpta*, have ranges that include this coastal region. In addition, all these other species either also occur in the northern coastal areas of Australia (*Carettochelys insculpta, Chelodina novaeguineae*) or have closely related (and possibly conspecific) relatives in northern Australia (*Elseya novaeguineae-E. dentata, Emydura*

subglobosa-E. kreffti, C. siebenrocki-C. rugosa) (Cogger, 1970; Burbidge, et al., 1974). *C. parkeri* is thus the only New Guinean species that neither occurs in northern Australia nor has a very close relative there.

The only previous mention of specimens referable to *C. parkeri* is in Cogger (1972). He assigns a photograph of *C. parkeri* to *C. siebenrocki* and describes the vermiculated head and reticulate carapace patterns of *C. parkeri* as being characteristics of *C. siebenrocki*.

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APPENDIX I—GLOSSARY

The italicized terms defined here are new terms first used in this paper. Other terms are defined by the authors cited below.

Anterior ventral marginals—the ventral surface of the anteriormost marginal scutes (usually marginals 1–4 on each side and the ventral surface of the nuchal scute) that are situated anterior to the two axillae (Fig. 3).

Apertura glossopharyngei—McDowell, 1964

Branchial I—Siebenrock, 1898

Branchial II—Siebenrock, 1898

Cavum acustico-jugulare—Gaffney, 1972

Cavum tympani—Gaffney, 1972

Condylus occipitalis—Gaffney, 1972

Corpus hyoideus—Siebenrock, 1898

Crista exoparacapsularis—McDowell, 1964

Crista jugalis—the sharp bony vertical crest which runs along the posterior third of the jugal and part of the postorbital, and serves as the anterior wall for the soft tissue "Mundplatte" (Fig. 6).

Crista supraoccipitalis—Gaffney, 1972

Crista ventralis hyoideus—a bony crest running lengthwise along the midline of the ventral aspect of the corpus hyoideus, from just posterior to the fenestra hyoideus to just anterior to the articulation with branchial II (Fig. 8).

Fenestra hyoideus—Siebenrock, 1898

Fenestra postotica—Gaffney, 1972

Foramen columellae auris—Siebenrock, 1897

Fossa temporalis superior—Gaffney, 1972

Incisura columellae auris—Gaffney, 1972

Post-otic antrum—Williams, 1954

Precolumellar fossa—Williams, 1954

Prefrontal spine—a bony spur of the prefrontals on the interior anteromedial margin of the orbit, directed posteriorly and ventrally towards the choanae (Fig. 6).

Processus exoparacapsularis quadrati—a

delicate bony extension of the quadrate reaching posteromedially to partially roof over the anterolateral aspect of the cavum acustico-jugulare and the medial third of the columella (Fig. 5).

Processus trochlearis pterygoidei—Gaffney, 1972

Pterygoid process of jugal—the portion of the jugal, posterior to the crista jugalis, which serves as the anterior extension of the processus trochlearis pterygoidei and on which the soft tissue "Mundplatte" rests (Fig. 4).

Pterygoid process of postorbital—the portion of the postorbital, posterior to the crista jugalis, which serves as the anterior extension of processus trochlearis pterygoidei and on which the soft tissue "Mundplatte" rests (Fig. 4).

Recessus scalae tympani—Gaffney, 1972

Spina parasupraoccipitalis— a spinous process from the supraoccipital projecting posteriorly along the dorsal surface of the exoccipital, embedded in a specific sulcus and appearing to split the exoccipital roughly in half (Fig. 16).

Sulcus jugalis—a groove, immediately posterior to the crista jugalis, which extends from jugal to postorbital and on which the soft tissue "Mundplatte" rests (Fig. 6).

APPENDIX II—EXPLANATION OF MEASUREMENTS USED

Carapace length is measured in an axial, not curved, line along the midline of the carapace. Carapace width is maximum width measured perpendicular to the carapace midline. Carapace height is the maximum height measured in the carapace midline. Plastron length is measured along the midline and does not include the anal spurs. Plastron width is measured across the axillary notches, regardless of whether this is maximum width or not. Length of dorsal and ventral surfaces of nuchal scute, length of intergular and length of fifth vertebral are lengths measured along the midline; widths of these scutes are maximum widths measured perpendicular to the midline. Width of anterior ventral marginals is the distance between the edge of the carapace and the area of skin attachment, measured at the midpoint of the second marginal. Depth of the anal notch is the ratio of the distance between the tips of the anal spurs divided by the distance from the apex of the notch to the imaginary line connecting the tips of the two anal spurs. Width of head is measured across the tympanic membranes, in a line perpendicular to the midline of the skull. Length of neck is the distance from the tip of the snout to the anterior edge of the carapace, measured along the midline.

Skull length is measured along the midline, from the anterior surface of the premaxillae to the posterior surface of the condylus occipitalis. Tympanic width of skull is measured across the middle of the cavum tympani, in a line perpendicular to the midline of the skull. Maxillary width of skull is measured at the widest part of the maxillae, perpendicular to the midline of the skull. Skull height is the maximum height at the level of the posterior border of the maxillae. Length of basisphenoid is measured along the midline; width of basisphenoid is the maximum width measured perpendicular to the midline of the skull. Length of hyoid is only the length of the corpus hyoideus, measured from the posterior border of the fenestra hyoideus to the articulation with branchial II.

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A Temnospondyl Amphibian from the Mississippian of Scotland

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A TEMNOSPONDYL AMPHIBIAN FROM THE MISSISSIPPIAN OF SCOTLAND

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ABSTRACT. The edopoid labyrinthodont, *Caerorhachis bairdi* (new genus and species), a specimen from Thomas Stock's collection and therefore probably from the locality of Loanhead, Midlothian, Scotland (Namurian A), has a skull structure that suggests affinities with the family Dendrerpetontidae. It has 31 presacral vertebrae, and limb proportions suggesting semiterrestrial habits, in contrast to the necessarily aquatic nature of most other known Mississippian labyrinthodonts. The vertebral structure is not of the rhachitomous type, but resembles the "protoreptilian" structure normally associated with primitive anthracosaurs. The vertebral anatomy of this animal is not consistent with the pattern expected according to Romer's theory of the evolution of the labyrinthodont centrum. Evidence from *Caerorhachis* and rhipidistian fish suggests that the specific pattern of the vertebral centra among Mississippian amphibians may be quite variable, and may not in itself be an adequate criterion for establishing the phylogenetic relationships of primitive tetrapods.

INTRODUCTION

During the late Paleozoic, amphibians were the dominant terrestrial vertebrates. The most common of the Paleozoic amphibians were the labyrinthodonts, so called because the dentine of their teeth was infolded in the form of a labyrinth. A more important characteristic of the group is that the centra of their vertebrae were formed from more than a single ossification per segment. The pleurocentrum, comparable to the definitive centrum of amniotes, forms the posterior part of the vertebral centrum and usually supports the neural arch. The intercentrum, a relatively insignificant ventral element in the vertebrae of lower amniotes and absent as a discrete element in the presacral region of mammals, was an important structural element in the vertebrae of nearly all labyrinthodonts. The intercentrum forms the anterior part of the vertebra and is expressed as the haemal arch in the caudal region.

The earliest labyrinthodonts, the ichthyostegids, are known from the latest Devonian. Remains of other labyrinthodonts are common in Pennsylvanian and Permian deposits, but the group is represented by less than a dozen genera in the fossil record of the Mississippian. Consequently, our concept of the early evolution of the group is based largely on evidence provided by the study of the Pennsylvanian and Permian forms.

Among the few labyrinthodonts from the Mississippian is a nearly complete skeleton of a previously undescribed form in the collection of the Museum of Comparative Zoology at Harvard University. The description of any Mississippian amphibian is of considerable importance, but the structure of the vertebrae of this specimen makes it of particular significance in understanding the phylogeny of Paleozoic labyrinthodonts.

ACKNOWLEDGEMENTS

We wish to thank the late Dr. Alfred S. Romer for allowing us to examine and make casts of the specimen of *Caerorhachis*. An interpretation of the structure of this animal

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would have been impossible without his extensive work on labyrinthodonts. We also wish to thank Dr. Farish Jenkins and Dr. A. W. Crompton for allowing us to continue the study of *Caerorhachis* after Dr. Romer's death. We would also like to extend our gratitude to Dr. Donald Baird, who prepared the specimen, and who was the first to recognize its importance. This work was supported by a grant from the National Research Council of Canada.

SYSTEMATIC DESCRIPTION

Class *AMPHIBIA*
Subclass *LABYRINTHODONTIA*

Order **TEMNOSPONDYLI**
Suborder **RHACHITOMI**

Superfamily EDOPOIDEA
Family DENDRERPETONTIDAE?

Caerorhachis, new genus

Type species: *Caerorhachis bairdi*.
Etymology: From the Greek "*kairos*" meaning suitable, and "*rhachis*" meaning spine, in reference to the vertebral column.

Diagnosis. Small edopoid amphibian, skull similar to that of *Dendrerpeton* except that the postparietals are relatively narrower and longer, there is not a well developed otic notch, and the pterygoids meet anterior to the interpterygoid vacuities; palate and medial surface of mandibles heavily denticulate; vertebrae "proto-reptilian"; pleurocentra large, horseshoe-shaped; intercentra smaller, crescentic; 31 presacral vertebrae.

Caerorhachis bairdi, new species

Etymology: The animal is named after Dr. Donald Baird, who first prepared the specimen and recognized its importance.

Diagnosis. Same as for genus.

Holotype. MCZ 2271, nearly complete skeleton preserved in associated blocks of coal shale. This specimen originally showed a limited exposure of bone, badly weathered, on the surface of the blocks. The external surface of the lower jaws and a large fragment of the skull roof were cast from the original bone. All of the bone was then removed from the specimen by soaking in a dilute solution of hydrochloric acid. Silicone rubber casts were then made. These casts, replicating the original bone surface with great clarity, formed the basis for this description.

HORIZON, LOCALITY AND HISTORY

According to Dr. Baird, the specimen was probably acquired by the Museum of Comparative Zoology in 1883 with the Thomas Stock collection of Scottish Carboniferous fish and amphibians. The specimen bore no label or written information when Dr. Baird prepared it in 1955. However, as he noted, the matrix closely resembles that of the Loanhead No. 2 ironstone, Limestone Coal Group, Namurian (E1), Upper Carboniferous. This is equivalent to the Upper Mississippian of North America.

DESCRIPTION

Skull. The dorsal surface of the posterior portion of the skull table was exposed prior to preparation, together with a natural cast of part of the medial surface of the right cheek and the ventral surface of the interorbital area. This area was cast before acid preparation (Fig. 1). Following preparation, the specimen was cast again (Fig. 2). A portion of the ventral surface of the fronto-nasal region can be seen on the cast, but palatal elements obscure much of the posterior part of the skull table. During preservation, part of the left cheek was folded under the skull roof; consequently, the left postorbital and quadratojugal are visible ventrally. Another bone, lying behind the skull, is probably part of the right quadratojugal.

Although the skull roof is incomplete, and much of the surface is exposed only in internal aspect, its general structure and most of its suture patterns may be restored with reasonable confidence. The outline of the skull is provided by the nearly complete palate. The general size and skull proportions resemble those of the primitive rhachit-

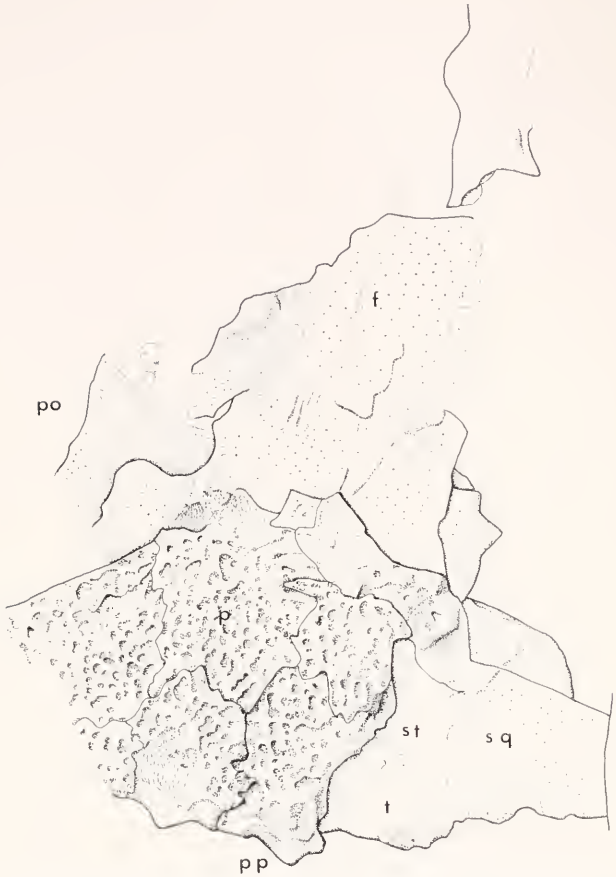


Figure 1. Skull roof of *Caerorhachis bairdi*, drawn from cast of original bone surface, × 3. (For abbreviations for this and following illustrations, see "Explanation of Abbreviations" at end of paper.)

omous amphibian *Dendrepeton* (Carroll 1967). The skull length is about 52 mm, which is roughly 1.4 times the width at the quadratojugal. The skull table is between 55 per cent and 60 per cent of the total skull width. The skull height was at least 35 per cent of its width at the quadratojugal. The quadrates are located only slightly behind the posterior margin of the skull roof as in *Dendrerpeton,* unlike the condition seen in *Edops* (Romer and Witter 1942), in which larger skull size has necessitated a relative increase in the size of the cheek region for the accommodation of a greater amount of adductor musculature. The posterior margin of the squamosal probably appeared concave when viewed laterally, but there is no evidence for the existence of a well defined otic notch. The center of the orbits is slightly anterior to the middle of the length of the skull.

The external surface of the dermal bones bears the typical temnospondyl pit-and-groove sculpturing. This is most clearly shown on the postorbital and quadratojugal. None of the bones shows evidence of grooves for lateral line canals. The skull table and cheek region appear to be suturally attached, as is the case in all temnospondyls, and in contrast to the condition in primitive anthracosaurs.

Weathering has damaged the bone surface of the skull table, muting the sculpturing and rendering the determination of su-

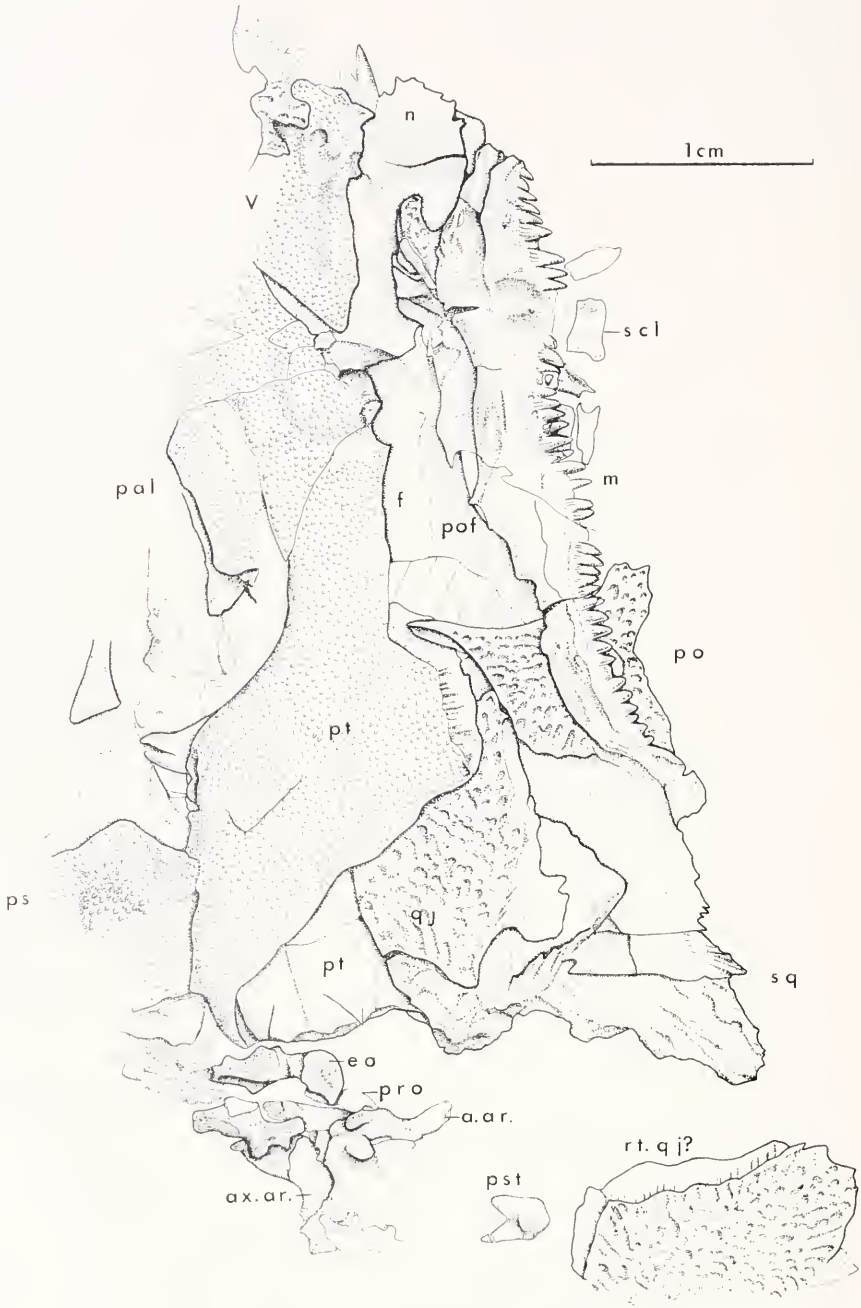


Figure 2. Disarticulated skull roof elements and ventral view of left side of palate of *Caerorhachis bairdi*, × 3.

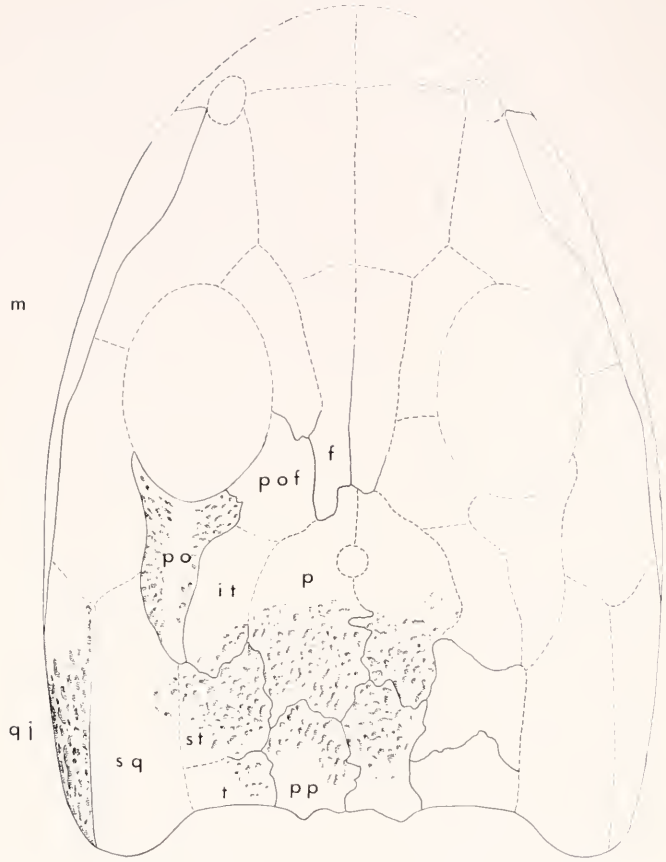


Figure 3. Reconstruction of the skull roof of *Caerorhachis bairdi*, × 2.

tures difficult. The tracing of sutures was also hindered by the loss of much of the bone of the anterior part of the table. Reconstruction of this area is based partially on impressions of the internal surface of the missing bone. The pattern of the skull table is shown in Figure 3. The postparietals are characterized by posterior lappets, as in *Dendrerpeton*, that presumably descend onto the occipital surface. These bones are relatively longer and narrower than those in *Dendrerpeton*. This is presumably a primitive characteristic, judging from the condition in other Mississippian temnospondyls such as *Greererpeton* (Romer 1969) and *Pholidogaster* (Panchen 1975). The tabulars are small and are separated from the parietals by the supratemporals. This is typical of temnospondyls and unlike the condition in anthracosaurs in which the tabulars are larger and make sutural contact with the parietals. The area of the pineal foramen is not preserved, although both the anterior and posterior limits of the parietals can be determined. The dorsal part of the right squamosal and adjacent skull roof are represented by a natural cast of the inner surface. Although the posterior borders of the right tabular and right squamosal are poorly preserved and incomplete, enough of these bones is present to indicate that the existence of a well developed otic notch is unlikely. The quadratojugal is surprisingly large, in marked contrast to that of *Dend-*

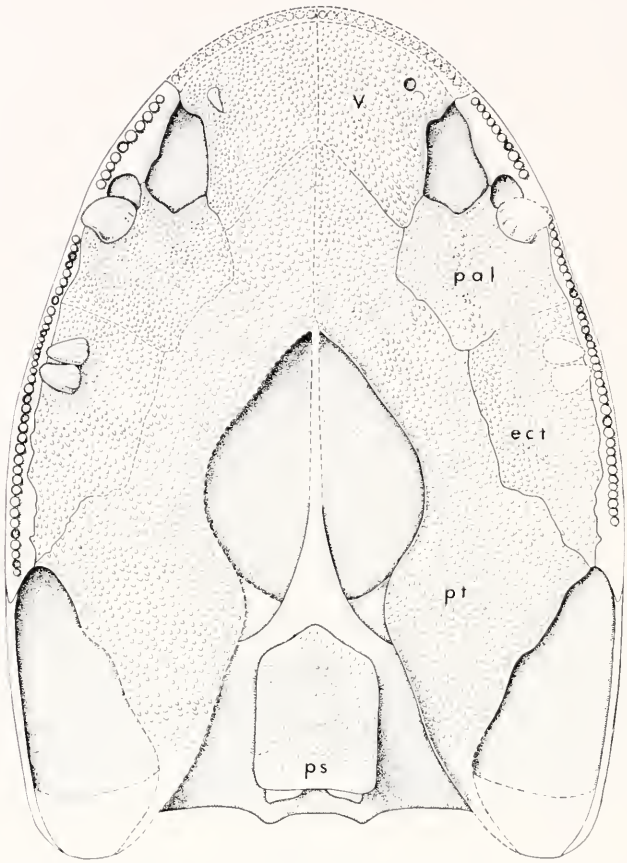


Figure 4. Reconstruction of the palate of *Caerorhachis bairdi*, × 2.

rerpeton, but no larger than that noted in other primitive labyrinthodonts such as *Edops, Greererpeton* or *Crassigyrinus* (Panchen 1973). The jugal cannot be identified. Only a few fragments of the anterior portion of the skull roof, of little use in reconstruction, are exposed in external view (Fig. 2). Part of the frontal-nasal region is exposed ventrally, but similarly is of little help in the reconstruction of the snout region. The outline of the anterior portion of the skull can be established from the dimensions of the palate and the length of the lower jaw. Apparently the snout was broadly rounded and the external nares were widely separated.

The left maxilla is exposed medially in association with the skull roof and palatal elements. The right maxilla remains in articulation with the margin of the palate (Fig. 5). Neither shows the tooth row in its entirety, but there appears to have been room for about 48 teeth in each maxilla. This is the same as the estimated number of maxillary teeth reported for *Dendrerpeton*. The medial surface of the left maxilla shows large depressions to accommodate the wide bases of the palatine and ectopterygoid fangs. Adjacent to the palatine fangs the margins of both maxillae appear to be devoid of teeth. Such a condition has not been described in any other labyrinthodonts. The tooth row of the left maxilla is about 10 per cent shorter than that of the

Figure 5. Right side of palate in ventral view and jaw rami in medial view of *Caerorhachis bairdi*, × 3.

right maxilla (Fig. 4) but shows evidence of distortion during preservation. The premaxillae are not preserved. However, the width of the snout indicates that each would have carried roughly 18 teeth, which is close to the count in *Dendrerpeton.*

Parts of the palate are preserved in two blocks. The left pterygoid, vomer, the dis-

Figure 6. External view of lower jaws of *Caerorhachis bairdi*, drawn from a cast of original bone surface, × 2.

placed left palatine (partially covered by the pterygoid), and the parasphenoid minus the anterior part of the cultriform process, are preserved in semi-articulated fashion (Fig. 2). The other block contains the right margin of the palate from the subtemporal fossa to a point slightly anterior to the internal naris. All elements are articulated except for the vomer, which has slipped slightly medially (Fig. 5).

The entire palate, except for the cultriform process of the parasphenoid, is covered in closely packed denticles. Sutures are occasionally indistinct, but slight displacement has revealed their positions in most cases. The pterygoids met anteriorly as they do in *Edops*. The basicranial articulation is definitely movable, as would be expected in such a primitive form. The cultriform process forms a slim rod, narrowing anteriorly. Because the remainder of the palate closely resembles that of *Dendrerpeton*, the process is restored as extending the entire length of the vacuities and inserting between the pterygoids anteriorly (Fig. 4).

The vomer, palatine and ectopterygoid each bear two fangs. Only one fang is actually present on the right palatine (the missing fang represented by an empty pit) indicating the regular replacement typical of early tetrapods. The vomerine fangs are slightly larger than the largest of the margi-

nal teeth, while those of the palatine and ectopterygoid are considerably larger than these teeth. All show typical labyrinthine infolding.

What can be seen of the medial margin of the left pterygoid indicates that the interpterygoid vacuities were relatively larger than those of *Edops*, but not as extensive as those of *Dendrerpeton*. The internal nares are large and rather square in proportion. They are quite similar in configuration and position to the internal nares of *Edops*, and quite unlike those of *Dendrerpeton*, which are relatively much larger and elongate. They are also widely separated, as is characteristic of temnospondyls. Anthracosaurs have a much narrower snout and consequently the space between these openings is much less. Fragments of the braincase can be observed in the same block containing the left side of the palate (Fig. 2). The occipital bones have become disarticulated from the rest of the skull and lie posterior to the parasphenoid. The exoccipitals are exposed in anterior view along with fragments of badly crushed bone possibly representing the remains of the otic capsule. Each exoccipital bears a rough, subcircular facet for the reception of the basioccipital. Dorsally, there is another facet that articulated with the opisthotic. Between these two articulating surfaces is a large vagus canal. A pleuracanth shark tooth lies nearby. The sphenethmoid region of the braincase has not been preserved. Sclerotic plates are present on the block containing palate and skull roof elements (Fig. 2).

Almost every feature of the skull suggests that *Caerorhachis* is an edopoid temnospondyl, similar in many ways to *Dendrerpeton*. The sculpturing is identical. The general proportions are very close, and the configuration of the bones on the skull roof is comparable. The supratemporal appears to be slightly smaller, and the intertemporal larger than in *Dendrerpeton*, but these bones are not perfectly preserved, making exact comparison of dimensions difficult. The temporal series is solidly fused to the cheek. The absence of a well defined otic notch appears to be the main feature distinguishing this animal from *Dendrerpeton*. Two other Mississippian labyrinthodonts, *Greererpeton* and *Pholidogaster* (Panchen 1975) also lack otic notches. These two closely related forms are primitive members of the family Colosteidae, a distinct lineage of secondarily aquatic labyrinthodonts unrelated to *Caerorhachis* and other edopoids. The absence of an otic notch may be a primitive feature of labyrinthodonts (Panchen 1975), although it has been generally assumed that this notch was derived more or less directly from the spiracular cleft of rhipidistians.

Lower Jaw. The poorly preserved lateral bone surface of the lower jaws shows sculpturing comparable to that present on the bones of the skull roof (Fig. 6). Unlike the jaw of *Dendrerpeton*, in which only the angular and splenial bear heavy sculpturing, the entire lateral surface of the jaw of *Caerorhachis* appears to be evenly covered by coarse sculpturing. Although most of the sutures cannot be followed, the sculpture pattern indicates that the arrangement of the bones is generally like that of a typical primitive temnospondyl. The splenials have unusually large lateral exposure, which is a primitive characteristic (Romer 1947). No lateral line canals are evident.

Acid preparation has exposed the medial surfaces. Although the rami have been badly crushed, and the sutures are sometimes difficult to distinguish from cracks on the bone surface, the medial aspect of the jaw can be reconstructed with reasonable accuracy (Fig. 7). The number and shape of the bones appear to be generally similar to those of typical temnospondyl labyrinthodonts. A shagreen of denticles similar to those already noted on the palatal elements completely covers the coronoids and prearticular. Such an extensive cover of denticles on the medial surface of the mandible is exceptional in labyrinthodonts (Romer 1947). A pair of parasymphyseal tusks, comparable in size to the palatal fangs, can

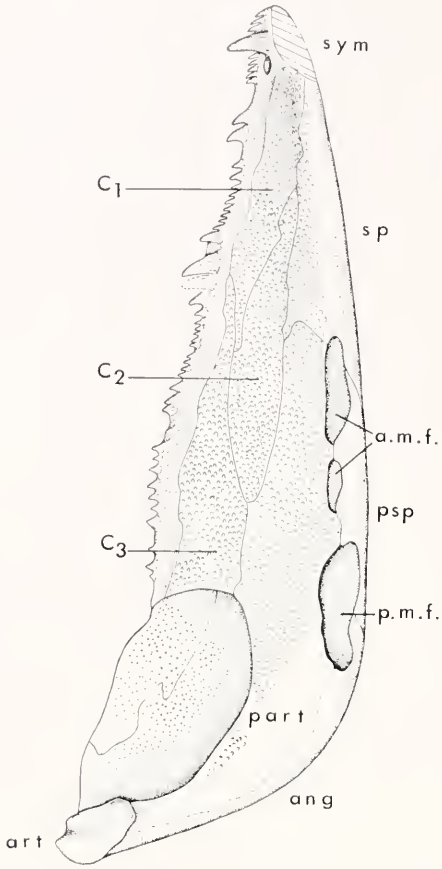


Figure 7. Reconstruction of the medial surface of the lower jaw of *Caerorhachis bairdi*, × 3.

be seen. Although often present in temnospondyls, these structures are not common in anthracosaurs, where they have been reported only in some Mississippian embolomeres (Romer 1963) and the Pennsylvanian genus *Gephyrostegus* (Carroll 1970). The dentary has room for between 60 and 65 teeth, all of which are simple conical structures, curved slightly backwards and showing labyrinth infolding. The teeth are significantly larger at two points in the tooth row. The first peak is located at about the 18th tooth, and the second at about the 32nd.

There are three meckelian fenestrae on the medial surface of the jaw. The most posterior is the largest, and is bordered posteroventrally by the angular, anteriorly by the postsplenial, and posterodorsally by the prearticular. Two additional fenestrae, located more anteriorly, are slightly smaller. They both appear to be bordered ventrally by splenial elements and dorsally by the prearticular.

If the short axis of the lower jaws was oriented vertically, the articulating surface of the articular bone would face mediodorsally, rather than directly dorsally. This indicates that, when in articulation, the jaw of *Caerorhachis* must have been tilted medially to a greater degree than in most labyrinthodonts. Romer and Witter noted a similar situation in *Edops*. Consequently, the medial surface faced obliquely dorsally toward the palate, and when the jaws were clamped shut they would have forced the prey up onto the palate. Presumably the thick and complete covering of denticles present on the palate and inner surface of the mandibles assisted the palatal fangs and marginal teeth in holding the prey.

Axial skeleton. The atlas-axis complex is preserved immediately behind the skull. The two halves of the atlas arch (Fig. 2) appear to have been coössified. The neural spine of the right half of the arch is a thin process, directed dorsoposteriorly, as described for *Eryops* (Moulton 1974). The anterior zygapophysis, for articulation with the proatlas, is located on a tubercle on the lower, anterodorsally facing surface of the spine. The posterior zygapophysis is not visible. The pedicle of the left half of the atlas arch is exposed in lateral view. The left proatlas lies close to the anterior zygapophysis. The pedicle of the left axis arch can be seen in medial view, exposing an extensive surface of articulation with the centrum. Unfortunately, no central elements of the atlas-axis complex have been preserved.

The remainder of the column is exposed in lateral aspect in semi-articulated fashion in the largest block (Fig. 8a, 9). It is not certain whether the most anterior of these

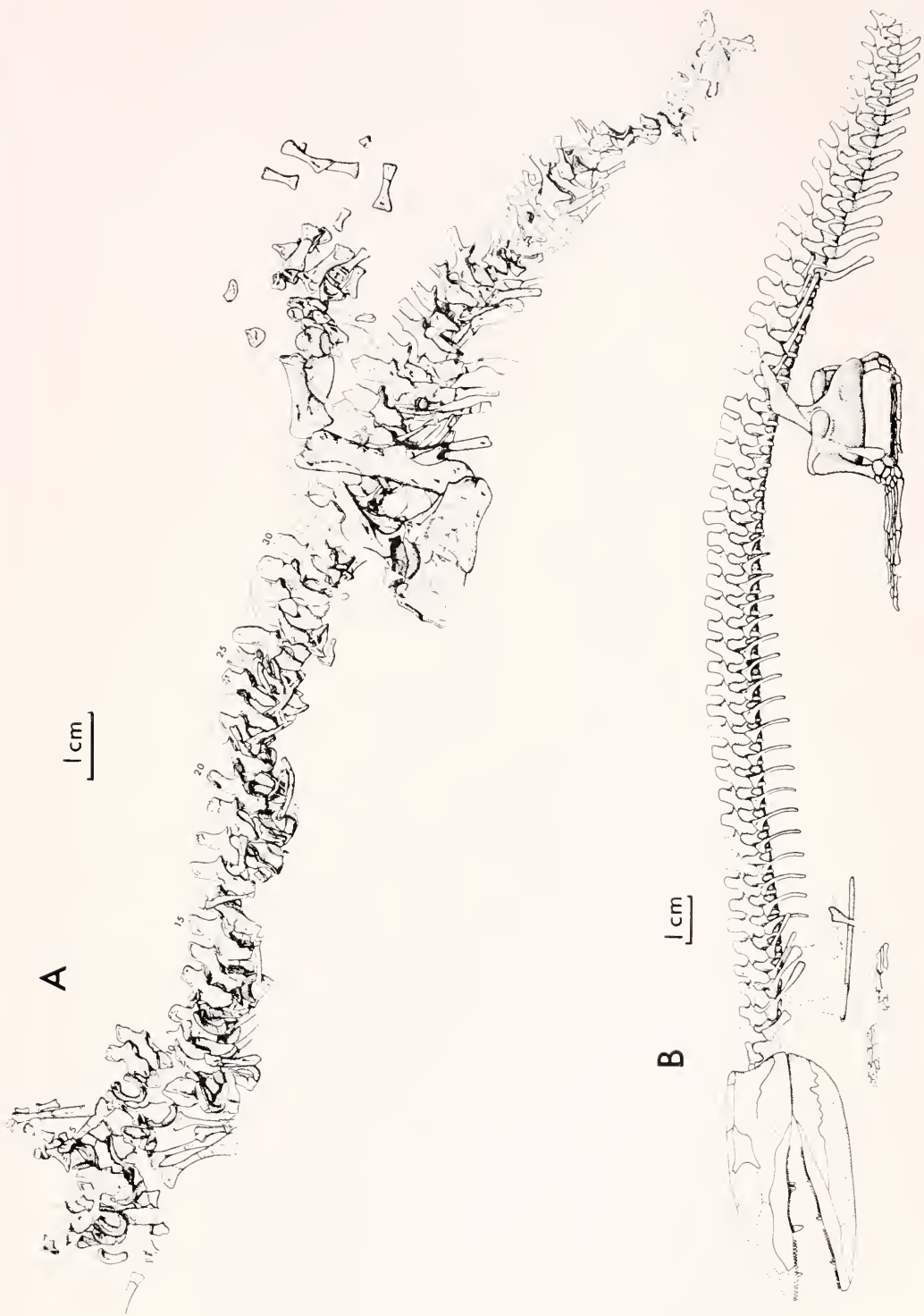
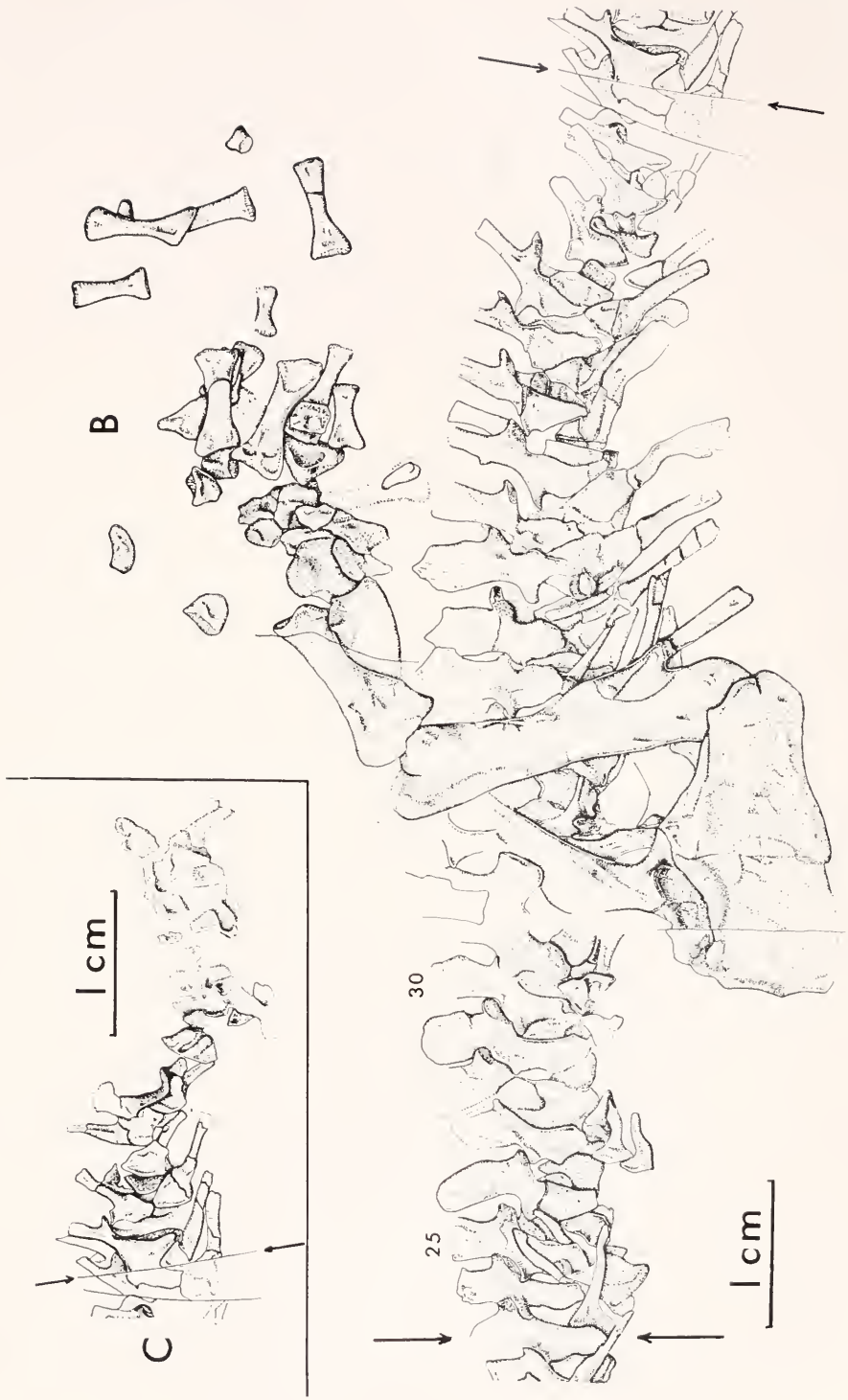


Figure 8. A, postcranial skeleton of *Caerorhachis bairdi*. This drawing is enlarged and presented in sections in Figure 9. B, stylized reconstruction of *Caerorhachis bairdi*. Scale indicated in both drawings.

Figure 9. Postcranial skeleton of *Caerorhachis bairdi*, reproduced in sections. A, anterior trunk; B, sacral region; C, tip of tail. Arrows indicate comparable position of successive sections. Numbers indicate approximate position of presacral vertebrae.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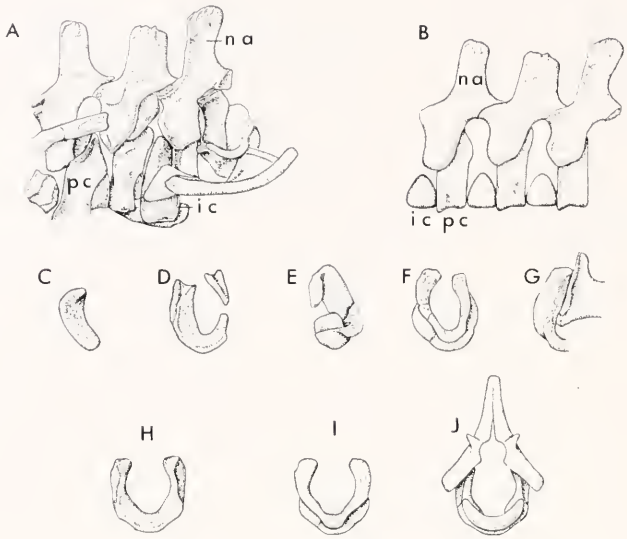

Figure 10. Elements of the vertebral column of *Caerorhachis bairdi*. A, 18th, 19th and 20th vertebrae, lateral view; B, restoration of 18th, 19th and 20th vertebrae, lateral view; C, ic 3; D, pc 3; E, pc 6; F, pc 7; G, pc 10; H, restoration of pc, anterior view; I, restoration of pc, posterior view; J, restoration of vertebra, anterior view. All × 2.

vertebrae represents the third cervical. The configuration of the associated ribs reveals that the first several vertebrae in the block are cervicals, and unless the animal has an unusually long neck, few if any vertebrae are missing in the series.

The pelvic girdle is disarticulated from the column and slightly displaced, so there is some question as to the position of the sacral vertebra. A structure which appears to be a sacral rib is present, but it is not clear whether it is associated with vertebra 31, 32 or 33. Haemal spines can only be identified definitely as far anteriorly as the 38th vertebra. Caudal ribs, however, are present as far anteriorly as the 33rd vertebra. This evidence points to the 32nd vertebra being the sacral, which makes the presacral column of *Caerorhachis* considerably longer than that of *Ichthyostega*, the oldest known amphibian. *Ichthyostega* has a presacral count of 23 or 24 according to Jarvik's reconstruction (Jarvik 1955). However, it may be significant that the presacral column of *Eusthenopteron*, a member of the group of crossopterygians giving rise to amphibians, is 32 (Andrews and Westoll 1970a). This count is also recorded in the oldest known reptile having a well articulated column (Carroll 1969).

The central elements of the vertebrae have been dissociated from each other and the arches, making reconstruction somewhat difficult, but providing additional information concerning the structure of the individual units. Study of the central elements visible along the column reveals two very distinct structural units (Fig. 10). One type is a simple, thin crescent when viewed anteriorly. These elements are similar to the intercentra of typical labyrinthodonts. The dorsal extension of the "horn" of the crescent would probably reach no further than midway in the height of the other central element. The other element, surely a pleurocentrum, is horseshoe-shaped when viewed end-on, and midventrally about the same length as the intercentrum. Its dorsal extension is greater, however, and on each anterodorsal surface is an articulating facet for the pedicle of the neural arch. A few of these elements remain in articulation with

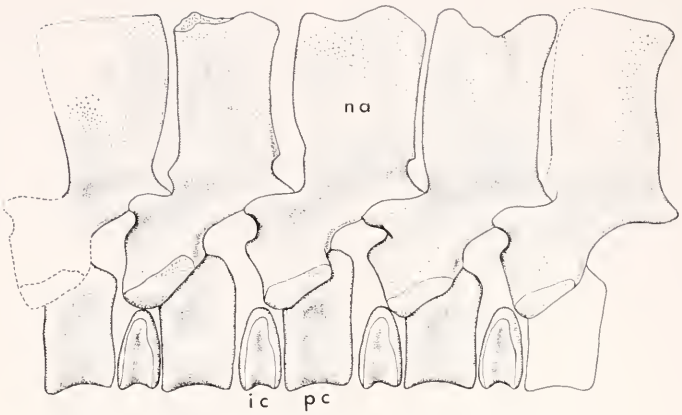

Figure 11. Dorsal vertebrae of *Proterogyrinus scheelei*, × 1.

their respective arches. Neural arches seven and eight each show an extensive unfinished area covering most of the medial surface of the pedicle. Although the arch and pleurocentrum were not solidly fused together, such a broad contact between the two elements must have allowed them to function as a single structural unit when in articulation. The anteroventral surfaces of the pleurocentra appear to be concave, matching well with the convex surfaces of the intercentra. This would produce a functional ball-and-socket joint between the intercentrum and the pleurocentrum behind it. Though the pleurocentrum supports the arch, it is quite thin-walled, only sheathing the notochord and probably not constricting it appreciably. Primarily notochordal vertebral columns are not uncommon among primitive labyrinthodonts, especially in small forms. In *Gephyrostegus* the pleurocentrum is also horseshoe-shaped and supports the neural arch, to which it is only weakly attached. The intercentra fit between the pleurocentra, surrounding the notochord ventrally.

Dendrerpeton, although unlike *Caerorhachis* in that it has typically rhachitomous vertebrae, is similar in having very thin-walled central elements which barely constrict the notochord. The vertebrae of the Upper Mississippian anthracosaur *Proterogyrinus* (Romer 1970) (Fig. 11) are quite similar to those of *Caerorhachis*, the main difference being the heavier construction of the pleurocentrum.

The neural spines are rectangular in lateral view, and many bear conspicuous grooves on their lateral surfaces, presumably indicating the points of ligament attachment. There is little regional variation in the morphology of the neural arches except with respect to the height of the spines. The spines of the arches immediately posterior to the sacrum are the tallest. The anterior cervicals are the shortest. The height of the spine of the seventh presacral, the most anterior vertebra in which the spine is completely preserved, is about 65 per cent of the height of the spines of the anterior caudals. The spine of the 28th presacral is intermediate in height, about 80 per cent that of the anterior caudals.

Although the vertebrae have been crushed laterally, it is apparent that the neural arches were not swollen, and the zygapophyses were close to the midline as in most other primitive amphibians and most reptiles. It is impossible to measure the angles of the zygapophyses accurately because of crushing, but the posterior zygapophyses appear to face ventrolaterally at an angle of roughly 45 degrees from the sagittal plane. Well defined articulating surfaces for the

Figure 12. Dorsal view of clavicle, interclavicle and forelimb elements of *Caerorhachis bairdi* found in association with the elements in Fig. 5, × 3.

attachment of ribs are not visible on the arches or on the central elements.

The cervical ribs are long and flattened. Both proximal and distal ends are expanded. They are double-headed, although a web of bone between the two heads tends to obscure this. Such large cervical ribs were probably necessary for the attachment of heavy neck musculature supporting the large head. The dorsal ribs are poorly preserved, but appear to have been short and rather fragile. They also appear to be two-headed, but the heads are approximately circular in cross section, unlike those of the cervical ribs. Only the first few caudal vertebrae have ribs associated with them. These ribs are even smaller and more fragile than the thoracic ribs. It is not possible to determine the nature of their articulating surfaces. They are gently curved and appear to have been directed posteriorly in life. Both the neural and haemal spines of the caudal vertebrae are quite long and the tail is consequently quite tall and appears laterally compressed. It was probably an effective swimming organ.

Appendicular skeleton. The anterior end of the interclavicle is preserved in dorsal view (Fig. 12), showing a fimbriated margin. None of the posterior end of the bone is preserved. The medial portion of the ventral plate of the right clavicle is exposed in dorsal view, in articulation with the interclavicle. It is poorly preserved, however, and no details of its structure can be determined. The scapulocoracoids are not present.

Next to the interclavicle can be seen the

proximal portion of the ulna, showing a well ossified olecranon. Adjacent is another bone, presumably the radius, and what could be a small fragment of the humerus. The size of these elements indicates that the forelimbs were small. The ulna is about 20 per cent the length of the skull. It is impossible to estimate the length of the humerus.

Two metacarpals and three toe bones are preserved with the other remains of the forelimb. No carpals are present. Two more metacarpals, two phalangeal elements and one terminal phalanx are preserved in association with the cervical vertebrae, and are presumably from the other manus. The hand has been reconstructed with four toes, but without any specific evidence.

The pelvic girdle (Fig. 9) is typical of primitive temnospondyls and is quite similar to that of the edopoid *Dendrerpeton*. Although the left half of the pelvic girdle is slightly crushed and the pieces somewhat displaced, the morphology of the structure is quite clear. The ilium, ischium and pubis are all well ossified, and the sutures are indistinct. A prominent buttress is evident above the acetabulum. Below the acetabulum the plate for muscle attachment, formed by the union of the pubis and the ischium, shows a definite concave surface. The obturator foramen is not visible.

The dorsal portion of the ilium is obscured by vertebral elements and the shaft of the femur. However, it is certain that it is a simple structure which passed posterodorsally in life to about the level of the zygapophyses of the vertebral column. There is definitely no anterior extension of the ilium, such as is present in most primitive anthracosaurs.

The left femur is preserved in dorsal view. It is basically a cylindrical structure with expanded ends, as is the case with most tetrapods. Most of the adductor crest is hidden from view, but a prominent internal trochanter projects from the anterior edge of the femur near its proximal end. The total length of the femur is about 50 per cent of the length of the skull. A well preserved tibia lies in articulation with the distal end of the femur. It is a stout bone, with a proximal end as wide as the distal end of the femur. The tibia is about 40 per cent of the length of the femur. The proximal end of the fibula is covered by the tibia. The distal ends of the fibula and tibia are of approximately equal width.

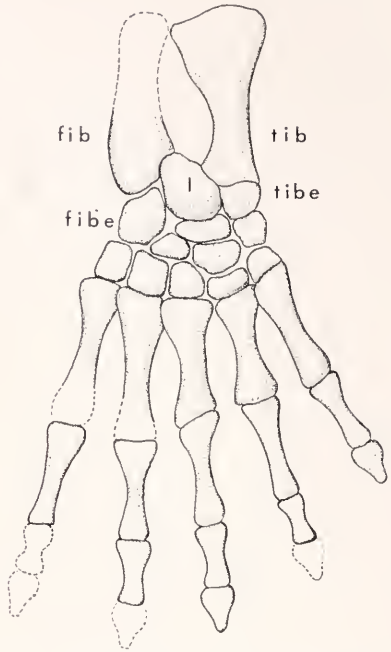

Figure 13. Reconstruction of the pes of *Caerorhachis bairdi*, × 2.

The tarsus appears to be essentially complete. Many of the bones are incompletely exposed, however, and their exact shape cannot be determined. The reconstruction of the foot (Fig. 13) shows a tibiale, intermedium, fibulare, four centralia of roughly equal size, and five distal tarsals, also of roughly equal size. The rest of the pes is disarticulated and scattered slightly, but there is no evidence to suggest that many of the bones are missing. Five metatarsals, eight proximal phalangeal bones, and two unguals can be clearly seen. Although it is conceivable that one more proximal phalan-

Figure 14. Ventral scales of *Caerorhachis bairdi* found in association with trunk vertebrae 20 through 30, × 2.

geal bone is also missing (which would give *Caerorhachis* a typical temnospondyl count of 2, 3, 3, 3, 3), it is highly unlikely that more elements have been lost. The phalangeal formula of *Caerorhachis* is here restored as 2, 3, 3, 3, 3; it certainly would not have been as high as that common in anthracosaurs (2, 3, 4, 5, 5).

A portion of the ventral armor is present in the block containing the vertebral column (Fig. 14). The individual scales can be seen as being quite long and stout. They collectively make a very heavy shield covering the ventral portion of the abdomen and probably extending from the interclavicle to the pelvic girdle.

HABITS

The absence of lateral line canal grooves on the skull roof and lower jaws and the presence of relatively large limb bones suggests that *Caerorhachis* was not tied to the water as were other known temnospondyl amphibians from the Mississippian such as *Greererpeton*, *Pholidogaster* and possible loxommatids. The presacral vertebral count is substantially lower than in the known members of these groups, although it is somewhat higher than that indicated for *Ichthyostega*.

Caerorhachis is here termed "terrestial" only in a relative sense. This genus may yet have spent much of its life in the water. It shows no specializations toward locomotion in this medium, such as are evident in all other known Mississippian temnospondyls and embolomeres, although the laterally compressed tail could have served as a swimming organ. One might visualize this animal spending much of its life in the damp mud on the margins of ponds or streams, feeding on stranded fish, or occasionally venturing into the water to catch aquatic larvae of other amphibians.

DISCUSSION

The general morphology of the skull and appendicular skeleton identify *Caerorhachis* as a primitive temnospondyl amphibian. As in typical temnospondyls, the tabular is a small bone and makes no contact with the parietal. The cheek is solidly fused to the skull table. The sculpturing on the dermal bones is of the typical temnospondyl pit-and-groove type. The internal nares are widely separated. The interpterygoid vacuities are quite wide, while those of anthracosaurs are only narrow slits. The ilium does not have the distinct anterior process characteristic of many anthracosaurs.

Primitive characteristics such as the presence of an intertemporal bone and a movable basicranial articulation, as well as the absence of lateral line canal grooves, indicate that this animal may be placed within the Superfamily Edopoidea. Furthermore, the general anatomy of the skull roof, palate and pelvic girdle shows that it is closely related to previously described members of the Family Dendrerpetontidae. The abscence of a well defined otic notch makes it awkward to include *Caerorhachis* within this family as currently understood, however. The nature of the vertebrae presents a much more serious problem to the classification of *Caerorhachis*. The vertebrae are well preserved and readily reconstructed. Their structure, however, is entirely different from that seen in *Dendrerpeton* and other edopoids, and is of a type totally unexpected in primitive temnospondyl amphibians.

The structure of the vertebrae has been the basis for the major subdivisions of Paleozoic amphibians according to all recent authors. The first workable classification of labyrinthodonts was developed by Watson (1919, 1926). He considered that the vertebrae of all known labyrinthodonts conformed to one of three structural stages and he used these differences as a basis for dividing the Labyrinthodontia into the Orders Embolomeri, Rhachitomi and Stereospondyli. In the Embolomeri both the intercentrum and the pleurocentrum are complete rings, forming a "double" centrum. The Rhachitomi have vertebrae composed of large crescentic intercentra and pleurocentra represented by small paired blocks situated dorsally, posterior to the intercentrum. In the Stereospondyli, the pleurocentra have completely disappeared, and the centra are composed of only cylindrical intercentra. At the time Watson wrote, most of the known Permian labyrinthodonts had the rhachitimous type of vertebrae and most of the Triassic forms stereospondylous. Little was known of the vertebral structure of Carboniferous labyrinthodonts, but the few

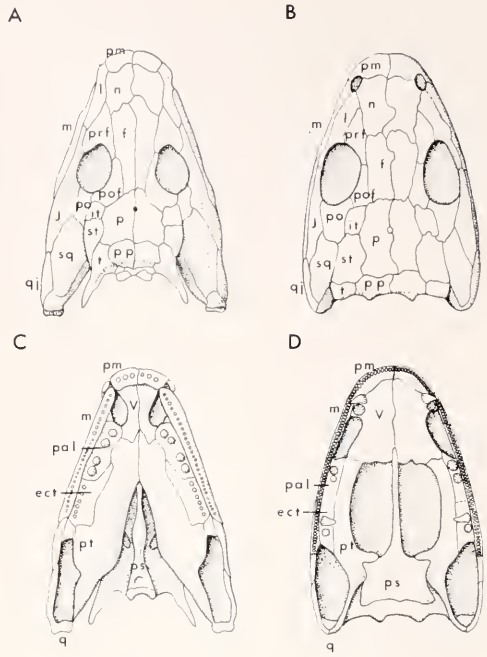

Figure 15. A comparison of the anthracosaur and temnospondyl skull. A and C, skull of *Paleoherpeton*, an anthracosaur, in dorsal and ventral views; B and D, skull of *Dendrerpeton*, a temnospondyl, in dorsal and ventral views. Not to scale. A and C from Panchen (1964). B and D from Carroll (1967).

specimens in which the columns were preserved showed an embolomerous pattern. On this basis Watson concluded that the embolomeres were the primitive labyrinthodont stock. He suggested they gave rise, some time late in the Carboniferous, to the rhachitomes on the one hand and reptiles on the other.

Romer (1947, 1966), to whom more information was available, revised Watson's classification. Romer used differences in vertebral structure as a basis for his new classification but also attached considerable importance to the association of certain features of the cranial anatomy with specific vertebral patterns. The relationship of the parietal and tabular is of particular importance. The tabular is large in embolomeres and other anthracosaurs and has sutural

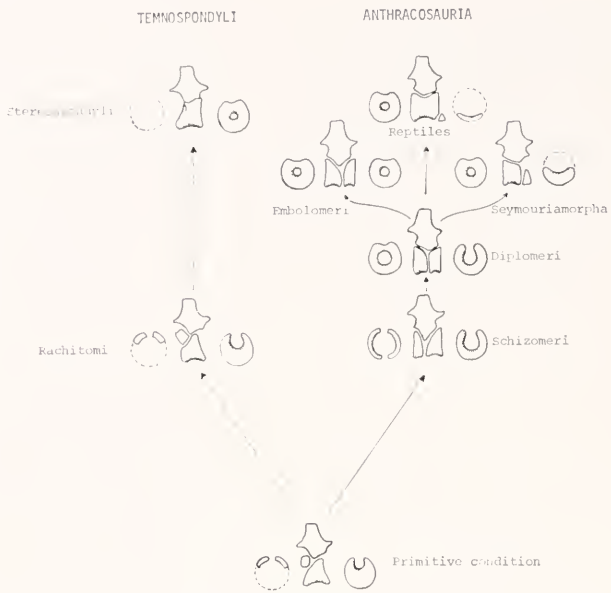

Figure 16. Romer's scheme for the evolution of the labyrinthodont centrum. Adapted from Romer (1966).

contact with the parietal. In temnospondyls, the tabular is small and separated from the parietal by the supratemporal, except in the Middle Permian genera *Intasuchus* and *Syndyosuchus* (Konjukova 1956).

In Romer's scheme (Fig. 16), the rhachitomous vertebral pattern is considered primitive for labyrinthodonts. The rhachitomes are suggested as having given rise to the stereospondylous pattern by elimination of the paired pleurocentra and enlargement of the intercentrum, and to the embolomerous pattern by fusion of the paired pleurocentra ventrally and dorsally to form a ring, together with dorsal elaboration of the intercentrum. Romer united rhachitomes and stereospondyls within the Order Temnospondyli. The embolomeres plus the specialized seymouriamorphs made up the Order Anthracosauria.

Evidence which has come to light since Romer's classification was first proposed has tended to support it. *Ichthyostega*, the oldest known amphibian (Upper Devonian), was identified by Romer as being a temnospondyl, although it was known only from skull remains when he first proposed his classification in 1947. This was apparently confirmed by Jarvik's (1952) description of the posteranial skeleton, although the vertebrae were closer in appearance to those of some rhipidistian crossopterygians than to those of typical rhachitomes. The loxommatids, common in the Carboniferous, were also included by Romer in the Rhachitomi because of their skull roof pattern, although the structure of the vertebral column was unknown in 1947. Baird (1957) later described rhachitomous vertebrae associated with the Carboniferous loxommatid *Megalocephalus*.

Romer (1964) found it necessary to hypothesize an intermediate stage, which he termed "schizomerous," to illustrate the transition from the rhachitomous vertebral pattern to that characteristic of anthracosaurs. In this condition, the pleurocentrum was still a paired element, as in rhachitomes, but the two halves extended more ventrally, almost meeting at the ventral midline. Fusion of these elements ventrally in subsequent forms would have produced a proper

anthracosaurian centrum. Further elaboration of the pleurocentra and reduction of the intercentrum could give rise to the reptilian condition. Romer suggested that *Pholidogaster*, a Lower Carboniferous labyrinthodont, displayed such an intermediate vertebral structure and could be considered as an ancestor of anthracosaurs.

At the time of the publication of Romer's 1964 paper, it seemed that all Paleozoic labyrinthodonts could be fitted into a single, simple phylogenetic progression, with the primitive rhachitomous pattern ancestral to all the vertebral diversity seen in the group. Subsequently, information has accumulated that necessitates re-examination of this scheme.

Recent preparation of the skull of *Pholidogaster* reveals that this animal is not at all closely related to embolomeres but, rather, is a primitive colosteid temnospondyl (Panchen 1975). *Proterogyrinus*, and the probably synonymous *Mauchchunkia* from the Upper Mississippian, were described respectively by Romer (1970) and Hotton (1970). Although this material pertains to an anthracosaur of great age and very possibly one ancestral to later members of that group, its vertebrae do not give any indication of the "schizomerous" structure that Romer hypothesized as being intermediate between the rhachitomous and anthracosaurian vertebral patterns. Instead, the vertebrae are almost reptilian in nature, each with a well developed, horseshoe-shaped pleurocentrum and smaller crescentic intercentrum (Fig. 11). This material makes it difficult to accept Romer's hypothesis that the anthracosaurian vertebral configuration was evolved from the rhachitomous or proto-rhachitomous pattern.

Questions have also been raised as to the suggested rhachitomous or proto-rhachitomous pattern of the vertebrae of *Ichthyostega* and *Eusthenopteron*. Thomson and Vaughn (1968) in their description of *Lohsania*, a rhipidistian with vertebrae somewhat similar to those of *Eusthenopteron*, suggested that the major vertebral elements in this animal represent both the pleurocentrum and the intercentrum in tetrapods. According to Thomson and Vaughn, the vertebral element identified by Romer as a pleurocentrum in rhipidistians such as *Eusthenopteron* and in *Ichthyostega* is actually an accessory arch element. However, exhaustive analysis of several rhipidistian genera by Andrews and Westoll (1970a, 1970b) confirms the identity of the pleurocentrum in these fishes.

Discovery of a more or less anthracosaurian vertebral structure in the oldest terrestial temnospondyl confuses the picture even more. There are a number of ways in which the vertebral pattern of *Caerorhachis* may be viewed. As the only known "terrestrial" temnospondyl amphibian from the Mississippian, it may simply be exceptional in its vertebral structure—a peculiar departure from a common rhachitomous pattern. Other closely related forms might resemble *Dendrerpeton* in vertebral as well as cranial structure. This interpretation conforms with Romer's suggestion that the rhachitomous pattern was basic to all temnospondyls.

One might, in contrast, emphasize the importance of the similarity of the vertebral structure of *Caerorhachis* to that of early anthracosaurs such as *Proterogyrinus* and *Gephyrostegus*. It is certainly of some significance that the earliest members of each of these respective lineages have nearly identical vertebral patterns. We were at one stage tempted to suggest that the common possession of a proto-reptilian vertebral pattern in these forms indicated that this was *the* primitive structure for labyrinthodonts. One can even interpret that structure in *Ichthyostega* as comparable. If the paired dorsal elements are not pleurocentra, the dominant crescentic element in that genus is functionally somewhat comparable to the horseshoe-shaped pleurocentra of *Proterogyrinus* and *Caerorhachis*. One immediate problem of this interpretation of *Ichthyostega* is that the intercentrum, an important element of all laby-

rithodonts, is thus unaccounted for. Our knowledge of higher temnospondyls makes it difficult to accept that the rhachitomous pattern was achieved by a reduction of the pleurocentrum from the pattern seen in *Caerorhachis*. A mechanical explanation, such as that proposed by Parrington (1967), might account for such a modification in large terrestrial derivatives, but does not explain the common presence of a rhachitomous pattern in aquatic loxommatids and colosteids as well as in edopoids (other than *Caerorhachis*) and eryopoids.

It remains much easier to retain the assumption that the rhachitomous pattern is fundamental to Pennsylvanian and Permian temnospondyl amphibians. This indicates that the pattern in *Caerorhachis* is distinctive, but this may be more a matter of superficial appearance than of functional significance. It must be emphasized that the ossified and fossilized elements of the vertebral column in *Caerorhachis*, *Gephyrostegus* and *Dendrerpeton*, and to a variable extent other small or primitive labyrinthodonts, do not occupy more than a small portion of the total structure. The column remains functionally notochordal, with an unknown amount of more resistant cartilage between and medial to the ossified elements. This situation is, in fact, not greatly different from that encountered in rhipidistians (Andrews and Westoll 1970a, b). In that group, the column is fundamentally notochordal, but with a considerable variety of vertebral ossifications. There is no obvious association of particular patterns with the various taxonomic groups. Apparently there are a number of different ways of solving similar functional requirements. This situation may pertain also among primitive and small amphibians. It may be expected that there would be a considerable variety of vertebral structures among Mississippian labyrinthodonts, particularly among the smaller forms. Different configurations may not, however, have much functional or phylogenetic significance, as long as the column as a whole is primarily notochordal. With increase in size and degree of vertebral ossification, the pattern increases in functional and phylogenetic significance. Within the Pennsylvanian the structure has become stabilized so that few, if any, exceptions are known to the pattern of intercentral dominance among temnospondyls and pleurocentral dominance in anthracosaurs. Within the Mississippian, however, it would seem possible that members of both of these orders, as established by the structure of the skull, could have a variety of patterns of the superficial vertebral ossification. The presence of one pattern would not necessarily preclude close relationship to forms with quite a different structure. At this stage, the amount and specific distribution of cartilage and bone at the surface of the notochord is clearly of less phylogenetic significance than it is in the Pennsylvanian and Permian.

The possibility of extensive plasticity within the vertebral patterns of Mississippian tetrapods indicates that it may be difficult, if not impossible, to establish any particular pattern as primitive, or to trace in any simple, straightforward way, the derivation of any of the specialized patterns from one another. The vertebral structure seen in *Caerorhachis* emphasizes these problems; further evidence may be expected from additional discoveries of labyrinthodonts from the Lower Carboniferous.

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EXPLANATION OF ABBREVIATIONS

a. ar.—atlas arch
a.m.f—anterior meckelian fossae
ang—angular
art—articular
ax. ar.—axis arch
c_1—1st coronoid
c_2—2nd coronoid
c_3—3rd coronoid
cl—clavicle
d—dentary
ect—ectopterygoid
eo—exoccipital
f—frontal
fib—fibula
fibe—fibulare
hum—humerus
I—intermedium
ic—intercentrum
icl—interclavicle
in—internal naris
it—intertemporal
j—jugal
l—lacrimal
m—maxilla
n—nasal
na—neural arch
p—parietal
pal—palatine
part—prearticular
pc—pleurocentrum
pm—premaxilla
pmf—posterior meckelian fossa
po—postorbital
pof—postfrontal
pp—postparietal
prf—prefrontal
pro—proatlas
ps—parasphenoid
psp—postsplenial
pst—pleuracanth shark tooth
pt—pterygoid
q—quadrate
qj—quadratojugal
rad—radius
rt. qj.—right quadratojugal
sa—surangular
scl—sclerotic plate
sp—splenial
sq—squamosal
st—supratemporal
sym—symphysis
t—tabular
tib—tibia
tibe—tibiale
ul—ulna
v—vomer

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